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Differential pollen dispersion and the interpretation of pollen diagrams

With a contribution to the interpretation of the elm fall

by

Henrik Tauber

With 2 Plates

I kommission hos
C. A. REITZELS FORLAG (JØRGEN SANDAL)
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PREFACE

Pollen preserved in lakes and bogs offers a comprehensive record of past vegetation. Attempts at deciphering these records provide a challenge to scientists in many fields, and have so far led to a remarkable disclosing of the broad lines of the vegetational history. Yet, it is evident that the comprehensiveness of pollen records is limited by the degree of dispersion of pollen. Moreover, the information on vegetational development inferred from such records will never be more precise than is our understanding of the processes by which pollen is brought to these basins. This was realized during discussions on possible interpretations of very detailed pollen diagrams carried out in the Department of Natural Sciences at the National Museum, Copenhagen. These discussions thus made the author consider the likely course and mechanisms of pollen transfer. In this way the here presented ideas gradually emerged.

Not being a botanist or a geologist help and advice in many respects have been necessary in order to pursue these considerations. For this help thanks are due first of all to J. TROELS-SMITH, SVEND JØRGENSEN, and BENT FREDSKILD at the National Museum for innumerable discussions on pollen analysis, for a sharing of their great experience with the author, and, not least, for their patience in answering all the odd questions of an uninitiated. This aid has been invaluable for the carrying on of the work. I am also greatly indebted to JOHS. IVERSEN and SVEND TH. ANDERSEN at the Geological Survey of Denmark for inspiring discussions on ecology and for helpful criticism of the ideas put forward. My thanks further go to many visiting pollen analysts with whom the ideas have been discussed. Possible untenable views on matters of botany or ecology are, however, not to be blamed on these advisers, but on a certain stubbornness in the author in sticking to his own views – without which, after all, a work like this could not have been carried through.

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1. INTRODUCTION

Pollen grains are liberated into the air in vast quantities. They are carried by air movements to the stigmas of the flowers, or eventually deposited on the ground and on lake surfaces. This transfer is a complex physical process, which can only be understood from a detailed knowledge of how and when pollen grains are released into the air, how they are transported by air currents in and above forests and over lakes and bogs, and how they finally settle out of the air and become incorporated in various deposits. Being dependent on transfer by air currents, the degree of dispersion will vary considerably with the size of the pollen grains, with the time of the year in which they are emitted, and with the physical structure of the vegetation. Pollen records preserved in lake and bog deposits must therefore be expected to give a more complex reflection of the vegetation around basins than is usually assumed in pollen analysis.

A large amount of data for air motion and for the transport of airborne particles in the size range of pollen grains has been gathered in recent years, foremost in fields like air pollution, dissemination of insecticidal aerosols, and travel of radioactive debris. This information, combined with available data for pollen dispersion, makes a re-evaluation of some of the fundamental concepts in pollen analysis possible, especially regarding:

a. the actual mode of transfer of pollen grains from source trees to lakes and bogs,
b. the extent of the areas which are effectively represented in pollen diagrams.

In these considerations pollen dispersion has been treated with a special view to the conditions prevailing in closed deciduous forests like those which covered most of the European lowlands in the Atlantic period.

The ideas of pollen transfer underlying the interpretation of pollen diagrams have never been described in detail. It appears, however, to be a common assumption in pollen analysis that pollen is chiefly brought to lakes and bogs in the way that considerable amounts of pollen grains are first carried to high altitudes by thermal convection currents, are spread over large areas, and later fall back on the earth in a more or less vertical descent. In addition some direct transfer of pollen from the shore or the border vegetation is usually assumed to take place. The supposed sedimentation of pollen grains was termed the "pollen rain" already in the first paper on pollen analysis by von Post (1916).

These ideas, which found some support in the investigations on pollen drift at high altitudes by Rempe (1937), have been expressed for instance by Erdtman (1943, p. 1) who describes transfer of pollen grains after release in the words: "Easily carried by the wind, some of them are transferred into higher regions by vertical air currents and remain there for days, weeks, or even months, before they settle bach to earth." Similarly Fægri and Iversen (1950, p. 34) write: "These enormous quantities of pollen are liberated, float in the air for a shorter or longer period, and are eventually sifted over the surroundings as the dense and even pollen rain."

In this simple model of pollen transfer, which seems to be tacitly assumed in most interpretations of pollen diagrams, little account is taken of wind velocities, wind turbulence, terminal velocities of fall of pollen grains, or the physical structure of the vegetation. A change in the pollen curves is therefore usually ascribed to a change in pollen production alone, either of the species in question, or of some other species, which, in a relative calculation, may influence the rest of the curves.

However, though it is well established that large amounts of pollen are carried to high altitudes by convection currents, a return in the form of something like a rain of pollen can not be maintained in view of the evidence from actual measurements of pollen drift, nor is it consistent with experiences on dispersion and deposition of airborne particles of the same sizes in fields like air pollution, dissemination of insecticidal aerosols etc.

Numerous experiments on pollen capture near the ground show that the number of pollen grains caught from air currents on a vertical surface, for instance an object glass covered with a sticky compound, at normal wind velocities are 10–20 times as big as the number caught on the same surface placed in a horizontal position. This indicates that pollen grains follow the wind currents and like these move most of the time in a predominantly horizontal direction. This follows also from the fact that common pollen grains have terminal velocities of fall in air of 1–10 cm/sec (pollen grains from deciduous trees: 2–6 cm/sec), while wind velocities near the ground usually are in the range of 1–10 m/sec, i. e. one to two orders of magnitude higher. Because of the comparatively small terminal velocities, most pollen grains have little tendency to settle under the influence of gravity, and their chief motion will be due to turbulent diffusion processes in the atmosphere. In these processes large numbers of eddies of a random character and of a range of sizes varying from centimetres to many metres will carry airborne particles in vertical and lateral directions in addition to the dominant downwind motion, and thus cause a continuous mixing and dilution with the surrounding air. In this way pollen grains carried to high altitudes are slowly mixed into the air currents near the ground and tend to follow these, until they are captured in the boundary layer immediately above the ground or around surfaces of other obstacles. In the boundary layer (a more or less stagnant layer of air extending a fraction of a millimetre or some millimetres above smooth surfaces) turbulence is suppressed, and nearly laminar movements parallel to the surfaces dominate. Particles captured in this layer will sink through it, following trajectories determined by wind speed and gravity. On rough surfaces the final departure from the air may be by turbulent impaction on surfaces rather than by gravitational settling through the boundary layer. The same process of transfer by eddy diffusion in air currents applies to local pollen which is not carried aloft. Pollen grains will fall vertically only in case of still air, which is very seldom during day-time when most pollen grains are deposited.

Hence, the term "pollen rain" is highly inadequate and ought to be replaced as a general term for pollen deposition. Both as a metaphor and a physical notion it has been misleading. Also the ideas of pollen transport connected with the concept of a pollen rain have to be modified and substituted by a more detailed model based on pollen transfer by eddy diffusion and a predominantly horizontal pollen drift near the ground. This is pursued in chapters 2 and 3. Since experimental data on the actual dispersion of airborne particles in forested areas are very scarce, only the broad outlines of a model subject to later modifications can be inferred at the moment. Such a tentative model should serve to indicate some of the consequences for the interpretation of pollen diagrams, which a change in the ideas of pollen flight carries with it, and to point out where further investigations are most needed.

With a chiefly horizontal pollen drift, pollen carried by the wind above the canopy of the forest can hardly be the main source of the large amounts of arboreal pollen actually deposited in small lakes and bogs, because with the most common wind velocities pollen from above the canopy will pass over the basins in a time much shorter than is required to fall a distance of 15–20 metres due to gravity, or to be mixed that distance downward by eddy diffusion. In these cases another way of transfer must be sought. In chapter 2 it is proposed, that this is via the trunk space of the deciduous forests. Air currents passing here have the most direct chance both of picking up pollen and of delivering it to the boundary layer above the surfaces of lakes or bogs.

For larger basins an increasing fraction of pollen from above the canopy will be carried down to the surface of the basin by eddy diffusion and by formation of vortices, and thus be mixed with pollen from the trunk space, the part from above the canopy being proportionally greater the larger the basin.

Finally, pollen will be brought down by rain, either as a true "rainout" where pollen grains are already contained in the droplets of the clouds, or as a "washout" due to a scavenging of the air by falling rain drops. In this way pollen in the whole layer below the bases of the clouds will be washed out with a high efficiency.

Pollen deposition is thus considered to consist of at least three components, pollen derived from the trunk space, from above the canopy, and from washout by rain, each of which are likely to have a different pollen spectrum.

With a more or less horizontal pollen drift another factor becomes of importance in pollen analysis: The physical structure and the denseness of the vegetation. This is because airborne particles in the size range of pollen grains will impact on branches and leaves when carried by the wind through the vegetation. Capture of airborne particles is a well known phenomenon in aerodynamics. In the size range of pollen grains this capture is differential in the way that big and heavy grains (e. g. pollen grains of beech, elm and lime) are filtered off to a much greater extent than small grains. In this way the spectrum of pollen carried through the vegetation will be highly distorted. A change in the denseness of the vegetation will also influence the velocities of air currents in the trunk space, and therefore the distance pollen is carried here. With a denser vegetation heavy pollen grains and pollen from trees growing at comparatively long distances from the basin will therefore be affected most. At minor basins a material change in the structure of the vegetation, in particular the shore vegetation, may therefore result in a sudden deflection of all the pollen curves independent of changes in pollen production.

A knowledge of the approximate extent of the area represented in a pollen diagram is indispensable for an ecological understanding of the diagram. Based on the assumption of a more or less even "pollen rain" it is usually supposed that pollen diagrams are of a certain regional character and register the vegetation effectively out to several kilometres from the basin.

The extent of the area represented will however, depend on the share of each of the three components in the pollen deposition. It is obvious that pollen carried through the trunk space will be of a very local nature due to the low wind velocities there, the main part of the pollen grains originating from within some hundred metres from the basin. Pollen brought down by rain may, on the other hand, be of a very distant origin, while pollen carried by the wind above the canopy will have an intermediate position in this respect, reflecting the vegetation within the range of some kilometres, though with a rapidly decreasing efficiency at increasing distances. Large differences in the extent of the area represented must therefore be expected between basins of different sizes. In a specific basin such variations may also be present at different levels in the pollen diagram depending on the denseness of the surrounding vegetation and on possible clearances around the basin. The extent of the area represented will, moreover, be different for different species depending on the size of the pollen grains and on the time of the year in which pollen is emitted.

Some of the consequences of this tentative model of pollen transfer in forested regions are illustrated by a discussion of the proper interpretation of the changes occurring in pollen diagrams from northwestern Europe at the transition from the Atlantic to the Sub-boreal period where a strong fall in elm pollen percentages is registered.

2. DIFFERENTIAL POLLEN DISPERSION

2.1. Atmospheric diffusion

The behaviour of stack effluents provides a visible picture of the processes of atmospheric diffusion. It shows the action of small-scale and large-scale eddies on the smoke trail which results in random crosswind and vertical displacements relative to an axis along the mean wind direction. These diffusion processes have been extensively studied, both experimentally and theoretically, throughout the last 30 years because of their importance in air pollution, in the dispersion of chemical warfare gasses, in travel of radioactive clouds, and in the dispersion of spores and the spreading of insecticidal aerosols. Based on field investigations a large number of formulae allowing a rough estimate and prediction of the dispersion and deposition pattern under average weather conditions have been developed and tested. The most generally used formulae of this type are those developed by SUTTON (1932, 1947, 1953) for dispersion of gasses emitted from point sources (e. g. a chimney) or from line sources (e. g. a crosswind line of chimneys). The formulae have also been adapted to include losses due to deposition of particles on the ground (GREGORY, 1945; CHAMBERLAIN, 1955). Comprehensive accounts of the dispersion processes and their meteorological aspects have been given by U.S. Weather Bureau (1955) and by World Meteorological Organization (1958); the most recent theoretical and experimental developments are summed up in FRANKIEL and SHEPPARD (Ed.) (1959) and in PASQUILL (1961); the application to biological fields, including a large body of experimental studies on spore dispersal, is given in GREGORY (1961).

According to the theories mentioned above, the rate of eddy diffusion in the atmosphere depends mainly on the wind velocities, the vertical temperature gradient, the vertical wind profile, and the surface roughness. Normally the temperature decreases with height in the troposphere. If this gradient attains values higher than 1°C per 100 metres (the dry adiabatic lapse rate), the atmosphere will be very unstable and large vertical displacements will take place. A lapse rate in the range 0–1°C per 100 metres corresponds to neutral and stable average conditions, while a temperature inversion (the increase of temperature with height) gives a very stable, thermally stratified, atmosphere, in which all vertical motions become suppressed.

Fig. 1 shows the behaviour of smoke plumes at different temperature gradients. Fig. 1a indicates the strong looping which occurs on warm clear days

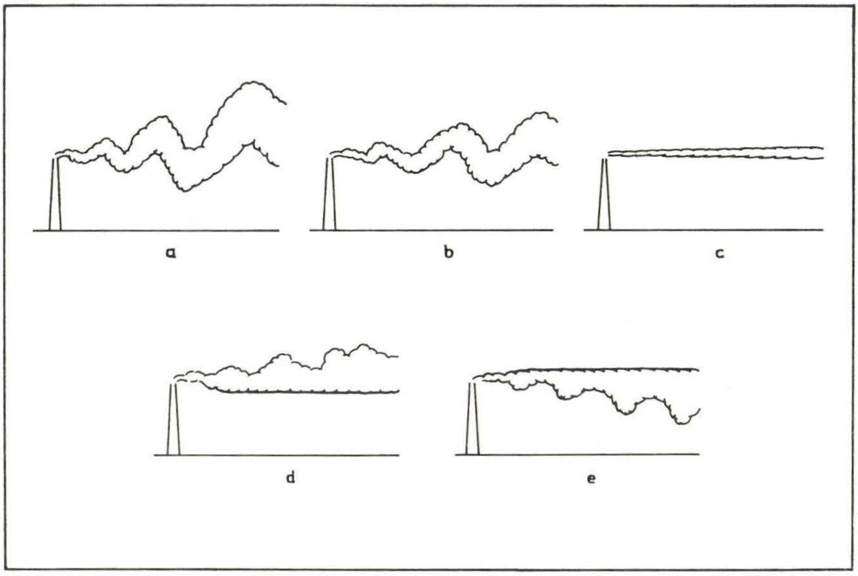

Fig. 1. Stack smoke behaviour under various meteorological conditions (after U.S. Weather Bureau, 1955).

with a high lapse rate and very unstable air. Due to convection the eddies attain great sizes, and the smoke trail is thrown upwards, downwards, and in lateral directions as a modulation on the downwind motion. Fig. 1 b shows the coning in neutral conditions corresponding to a warm cloudy day where the sizes of the eddies are more moderate, and Fig. 1 c pictures the fanning that occurs in a stable, stratified atmosphere under inversion conditions, where eddies are suppressed and the smoke trail may travel for many kilometres with very little widening. Fig. 1 d and 1 e indicates plume behaviour in more special cases. Fig. 1 d shows lofting which may occur in the evenings on warm days, when the air layers closest to the ground are cooled, while the air above retains its temperature, thus creating an inversion near the ground and normal lapse rate conditions above. Fig. 1 e finally shows the case of fumigation which is common in mornings, when the night inversion is broken down by the sun in the layers closest to the ground while the inversion layers above act as a lid to vertical displacements. In this case airborne particles in the lowest layer of the atmosphere are brought to the ground very rapidly, and unpleasant or dangerous concentrations of contaminants may be deposited close to the source.

The atmosphere thus behaves very differently with different temperature gradients. Pollen emitted at different times of the year (from February to October), when different weather types dominate, will therefore be subject to dispersion processes of varying types and intensities, and consequently must be dispersed over different distances.

Pollen is emitted preferentially on warm days with a low degree of humidity, i. e. in weather conditions corresponding to cases like those depicted in Fig. 1 a and 1 b. SUTTON's formulae (1947, 1953) for the dispersion in a free atmosphere over a smooth field in these cases are mentioned below because they give some quantitative ideas of the rate of dispersion in the atmosphere and will be used in the following sections. In general they allow a prediction of mean atmospheric concentrations, which, for average weather conditions and moderate distances, will agree with experimental values within about a factor of 2.

In the case of a *continuously emitting point source situated at ground level*, the average concentration immediately above the ground on an x-axis downwind along the mean wind direction, and on a y-axis at right angles to this, can be calculated from the equation

$$\chi_{(z,y,0)} = \frac{Q}{\Pi \, C_y \, C_z \, u \, x^{2-n}} \, e^{-} \frac{y^2}{C_y^2 x^{2-n}} \tag{1}$$

Here Q is the source strength in number of particles emitted per sec or the amount of gas emitted in g/sec, C_y and C_z are diffusion coefficients for lateral and vertical directions, respectively, and can be evaluated from meteorological observations, u is the mean wind volocity, n expresses the degree of turbulence and is determined from the vertical wind profile (which is related to the lapse rate), x is the distance downwind from the point source along the x-axis, and y is the lateral deviation.

If only the concentrations along the x-axis, which are the highest concentrations, are considered, (1) is reduced to

$$\chi_{(x,0,0)} = \frac{Q}{\Pi \, C_y \, C_z \, u \, x^{2-n}} \tag{2}$$

The turbulence parameter n varies from 0.15–0.20 in the case of a high lapse rate, is 0.25 in neutral conditions, and 0.3–0.4 under inversion. In neutral conditions $C_y = 0.21 \text{ m}^{n/2}$ and $C_z = 0.12 \text{ m}^{n/2}$ (SUTTON, 1947; CHAMBERLAIN, 1955) for the lowest layers of the atmosphere. It follows from (2) that the maximum concentration from a continuous point source at ground level occurs at the source itself, while the concentration downwind decreases with a power of the distance x from the source which is close to, but always less than, 2, i. e. a very rapid decrease with distance.

If the *continuous point source* is *situated at a height h* above the ground, the approximate concentrations along the x-axis become

$$\chi_{(x,0,0)} = \frac{Q}{\Pi \, C_y \, C_z \, u \, x^{2-n}} \, e^{-} \frac{h^2}{C_z^2 \, x^{2-n}} \tag{3}$$

In contrast to (2) this formula gives a zero concentration at the source itself, followed by a very slow and later a rapid increase with distance, until a maximum is reached at a distance d_{max} from the source equal to

$$d_{max} = \left(\frac{h^2}{C_z^2} \right)^{\frac{1}{2-n}} \tag{4}$$

The distance of maximum concentration from an elevated source is thus only a function of the source height h, the vertical diffusion coefficient C_z, and the turbulence parameter n. The maximum concentration at this distance decreases with the square of the height of emission, a relationship which is well known from the construction practice for chimneys (BOSANQUET and PEARSON, 1936).

A line source may approximate the type of source in pollen analysis more. The concentration from such a source will decrease more slowly with distance because no lateral dilution takes place. From a *continuous elevated crosswind line source at height h*, the ground level concentrations along the x-axis become

$$\chi_{(x,0,0)} = \frac{Q}{\Pi^{\frac{1}{2}} C_z u x^{\frac{2-n}{2}}} e^{-\frac{h^2}{C_z^2 x^{2-n}}} \tag{5}$$

In this case Q is the number of particles emitted per second and per metre. The distance of maximum concentration from the source becomes a little longer, and the maximum concentration at this distance somewhat greater than for a point source. The formula for the distance of maximum concentration is

$$d_{max} = \left(\frac{2 h^2}{C_z^2}\right)^{\frac{1}{2-n}} \tag{6}$$

Values of d_{max} for a point source (4) and a line source (6) at different heights and at various degrees of turbulence are given in Table I.

In the formulae above it is assumed that losses due to deposition are negligible compared to the concentration in the atmosphere immediately above the ground. If deposition is important, as is the case for pollen grains, formulae (2), (3), and (5) have to be modified slightly. For a source at ground level this modification may be accomplished (CHAMBERLAIN, 1955) by replacing the constant source strength Q with a quantity $Q_{(x)}$ equal to

$$Q_{(x)} = Q e^{-\frac{4 v_g x^{n/2}}{n u \Pi^{\frac{1}{2}} C_z}} \tag{7}$$

In this expression it is assumed that the deposition at any distance from the source is proportional to the concentration in a layer of the atmosphere immediately above the ground. The quantity v_g denotes the velocity of deposition, which in most cases will approximate the terminal velocity of the particles, but in cases of high turbulence may be greater than this. It follows from (7) that the loss due to deposition, and the deposition rate, will be much greater for large and heavy pollen grains than for small pollen grains. Heavy pollen grains will therefore be dispersed over much shorter distances. For sources at a height (h) a somewhat more complicated expression is necessary in order to account for the fact, that losses due to deposition do not take place before significant quantities of the emitted particles have reached ground level, i. e. roughly at distances equal to or greater than d_{max} (CHAMBERLAIN, 1955). Also in this case heavy pollen grains will be rapidly deposited and therefore dispersed over much shorter distances than small pollen grains.

Table I

Height	Point source			Line source		
h	d_{max}			d_{max}		
	$n = 0.20$	$n = 0.25$	$n = 0.30$	$n = 0.20$	$n = 0.25$	$n = 0.30$
	$C_z = 0.20$	$C_z = 0.12$	$C_z = 0.07$	$C_z = 0.20$	$C_z = 0.12$	$C_z = 0.07$
metres	metres	metres	metres	metres	metres	metres
5	35	70	150	50	110	230
10	80	160	340	110	220	520
20	170	350	770	240	510	1150
30	260	550	1260	380	810	1870
40	360	760	1750	530	1140	2630

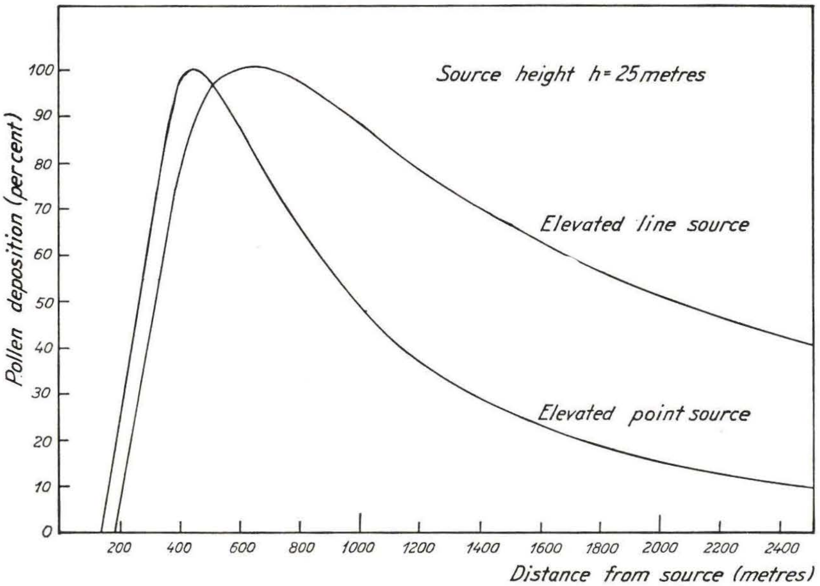

Fig. 2. Theoretical pollen deposition from an elevated point source and an elevated line source under average meteorological conditions. The deposition is expressed in percentages of the maximum deposition for each source type. Source height h = 25 metres, meteorological parameters $n = 0.25$, $C_z = 0.12$ $(\text{metres})^{1/8}$, $u = 3$ m/sec, $v_g = 0.02$ m/sec.

Concentrations downwind along the x-axis from a continuous elevated point source (3) and a continuous elevated line source (5), both corrected for losses due to deposition, are shown in Fig. 2 for light pollen grains. The curves are calculated for a source height of 25 metres, a mean wind velocity of 3 m/sec, and an average turbulence of the atmosphere (characterized by $n = 0.25$, $C_y = 0.21$ $\text{metre}^{n/2}$, and $C_z = 0.12$ $\text{metre}^{n/2}$). It is seen that practically no deposition takes place in the first 200–300 metres from the source, simply because the plume, at average turbulence, does not reach ground level within these short distances. These findings are in accordance with several investigations of deposition from stacks, where particles in the size range of pollen grains usually are found to be deposited at distances greater than 10 times the stack height (see GREEN and LANE, 1957).

SUTTON's formulae have been applied to the dispersion of spores in open areas (GREGORY, 1945, 1961), to the dispersion of pollen grains from cereal fields (BATEMAN, 1947), and to the dispersion of pollen from various forest trees (WRIGHT, 1952). In all cases a fair agreement with experimental values was found. GREGORY (up cit.) also tested the old dispersion formulae of SCHMIDT (1918). They did not conform with field experiments.

A direct application of these dispersion formulae to pollen analysis in general is difficult. First, natural sources are much more complex than the point and line sources considered above; natural sources usually being area or volume sources with varying heights of emission and with an unknown degree of refloatation. Secondly, meteorological conditions through long sampling periods (in the range of years) include a number of large scale phenomena such as frontal passages, orographically induced convective activity, and the formation of lee waves and rotor systems produced by terrain at certain wind velocities, all of which are variables that will change in frequency and intensity during the year and in different climatic periods. Thirdly, both the airflow and its turbulence, and the filtration of pollen grains by the vegetation, is highly influenced by the structure and denseness of the growth. It is however obvious that the source strength Q (i. e. the pollen production) is only one of a great number of variables which determine the final number of pollen grains deposited. Though not directly applicable to pollen analysis in general the formulae may be used to give orders of magnitude for the rate of dispersion in idealized situations and in specific cases. In this way they are used below.

2.2. Dispersion from a forest edge

A considerable number of measurements of pollen dispersion from single trees or from a forest edge out over an open area is given in the literature (REMPE, 1937; WOLFENBARGER, 1946, 1959; BUELL, 1947; WRIGHT, 1952; ANDERSON, 1955; PERSSON, 1955; SCHMITT, 1955). In a few cases pollen deposition attains a maximum at some distance from the source, as in Fig. 2 (REMPE, 1937, p. 110 and 116; PERSSON, 1955). Here the pollen drift was measured by impaction on cylinders or spheres, and the figures have to be corrected for different wind velocities at increasing distances from the forest (see chapter 3). In most other cases the maximum concentration or deposition occurs in the forest itself or at the forest edge, with a steadily decreasing deposition with distance from the forest edge. This is contrary to what would be expected if the pollen originated from above the canopy alone.

According to the curves in Fig. 2 pollen grains released at a height of 20–30 metres, in an atmosphere of average turbulence, will not be brought to the ground by eddy diffusion before som hundred metres from the place of release. Only if a rapid downward mixing of air in connection with vorticity occurs to the lee of a forest, or if special circulation mechanisms are established, would it be possible to get a large fraction of pollen from above the canopy deposited directly behind a forest.

Wind velocities to the lee of a vegetation are known from investigations of the effect of shelterbelts. Both in field tests and in wind tunnel experiments it is shown that if the shelter is impermeable to the wind, large vortices and eddies may be formed to the lee, and the shelter effect will only extend to short distances. In such cases a rapid down-mixing of air takes place. In contrast, a penetrable shelter will give few vortices and a reduced wind velocity out to distances of 20–30 times the height of the shelter (NÄGELI, 1943, 1946; JENSEN, 1954; GLOYNE, 1954; CARBORN, 1957). Similar conditions and a similar distance of lee are found for the shelter behind a forest (WOELFLE, 1936; NÄGELI, 1953;

JENSEN, 1954). Wind velocities equal to those above the canopy are usually not found until distances of 20–30 times the height of the forest. The gradual increase of wind velocity from the forest edge and outwards indicates that a gradual downward mixing of air takes place behind a forest. In the abscence of vortices it will, however, take some time before air from above the canopy is mixed down to ground level, especially since the colder air from the interior of the forest will stretch out underneath the usually warmer air from above the canopy.

The formation of vortices at forest edges has been studied directly by the use of smoke balls which make the air motion at the forest edge visible (WOELFLE, 1936 and 1950). Summing up, WOELFLE (1950, p. 51) writes: "Neben den Messungen mit Schalenkreuzwindmessern wurden auch Beobachtungen mit künstlichen Rauchwolken gemacht. Dabei wurde nie die Ausbildung von Luv- oder Leewirbeln festgestellt. Während an luft-undurchdringlichen Hindernissen Wirbeln regelmässig auftreten, gibt der immer etwas durchgeströmte Wald offenbar nicht die nötigen Voraussetzungen für diese Erscheinung". ZENTGRAF (1952) similarly found no vortices to the lee of a forest, and PFEIFFER (1938) found only small rolling vortices which disappeared at distances of 10 metres from the forest. It thus seems that the wind shear to the lee of a penetrable forest will be reduced so much, that the development of larger vortices and a rapid downward mixing of air is not the rule.

Circulation mechanisms are associated with a different heating of adjacent areas, which produce a temporary rise of portions of air (thermals) over warm surfaces, and a subsidence of air over colder areas. These phenomena are known from the experiences of glider pilots and from measurements of thermals (LUDLAM and SCORER, 1953; YATES, 1953). The hot surfaces are predominantly sun-facing slopes with a dry or no vegetation. The downward movement of air in the neighbourhood of thermals is usually reported to be slower than the up-currents, because the sinking of air seems to take place over wider areas. In the case of large differences in temperature the turnover of air may produce local winds like the land and lake breezes, or valley and slope breezes. Due to evaporation the canopy of a forest will not be heated as much as a field or a heath, and the circulation mechanism will therefore be suppressed over a closed forest; moreover, it is doubtful whether the downward motion, if occurring over a lake in forested areas, will extend to layers below the tree crowns, i. e. the altitude where the convection originates. In any case, a possible circulation effect will be reduced the smaller the lake is, and it is not likely to be so permanently established, that it can account for the large amounts of pollen which are actually deposited in small lakes throughout the period February to October, when pollen is emitted. Nor can circulation be expected to account for the deposition of pollen on small bogs, since parts of the bog surface may well be heated more than the surrounding forests, and in such cases will act rather as a chimney with rising air.

These considerations lead to the conclusion, that, in contrast to what is generally assumed, pollen carried above the canopy is not likely to be the main source of the pollen deposited in minor lakes. Instead, it is suggested, that the main part of the pollen, which is deposited within a few hundred metres from a forest, is carried with the air currents through the trunk space.

Contribution of pollen from the trunk space in conjunction with pollen from above the canopy would immediately explain the usual form of the curve depicting pollen deposition with increasing distance from a forest. Most often the concentration or deposition falls off rapidly out to distances of a few hundred metres from the forest as if it derived from a source situated close to ground level. In this range pollen grains from the trunk space are probably the main source. At greater distances pollen from above the canopy will dominate, and the deposition decreases very slowly with distance, as would be expected from an extended area source which will give a slower decrease than a line source. The deposition per unit area at distances corresponding to the flat part of the curve will be small compared with the deposition at the forest edge, if the source forest is small or the male flowering is poor, and large if the source forest has a great extent and the pollination is rich. This has been directly measured for a pine forest in two subsequent years, one with a medium pollination, the next with an abundant pollination (PERSSON, 1955; ANDERSON, 1955).

2.3. Dispersion through the trunk space

Very large quantities of pollen are brought to the ground in a forest. Pollen concentrations in the air of the trunk space will therefore reach high values during the periods of pollen emission, and possible wind currents here may disperse large amounts of pollen through the forest. The crucial point is therefore: Do the wind currents in the trunk space attain such velocities that substantial amounts of pollen are carried out of the forest by these currents?

Wind velocities in forests have been measured by GEIGER and AMANN (1931), PFEIFFER (1938), WOELFLE (1942), ZENTGRAF (1952), and NÄGELI (1953). These measurements give the following picture of air motions in a closed forest. When the wind blows towards a forest, the air flow is split in two parts, one being forced up above the crowns by the windward edge, the other proceding through the trunk space. Wind velocities in a forest will depend highly on the structure of the forest and, in particular, on the amount of undergrowth present; typical velocities at the windward edge, inside the forest and in the case of little underwood, is 40–70 per cent of the free wind velocity. Inside the forest, the wind velocities in the trunk space rapidly decrease until a constant value is reached, usually at a level of about 10–20 per cent of the free wind velocity. Shortly before the lee egde of the forest the wind velocity increases again to about 20–30 per cent of the free wind velocity and a further increase follows immediately outside the forest. Before leafing wind velocities in a forest will be 50–100 per cent higher than those quoted above.

As the wind sweeps over the crowns, two effects are acting on the air below: A suction out through the canopy, and a downward mixing from above caused by vortices formed by the passage over the rough canopy. The downward mixing takes place both directly through the foliage and, particularly, through openings in the canopy. Both effects add momentum to the air currents in the trunk space. Constant wind velocities in the interior of a large forest are reached, when the addition of momentum from above the canopy is balanced by the resistance to the flow through the vegetation. When the resistance to the air flow decreases, as shortly before the lee edge and in openings, the velocity of the wind currents therefore increases again. The downward mixing of air through the canopy will also add pollen grains from above the crowns to pollen carried in the trunk space. The main part of these pollen grains will come from the direct vicinity of the place of down-mixing, but a fraction will be long distance transport (see section 2.4.). In each passage of airborne pollen through the canopy a differential filtration will take place (see section 3.2.), and a depletion of heavy pollen grains will result.

GEIGER and AMANN (1931) measured vertical wind profiles in a large oak forest at two different spots, one with only a little undergrowth of small beech trees, and the other with a rather dense underwood of taller beeches. The distance between the two spots was less than 100 metres and the undergrowth at the second profile may possible have had some influence on the air flow at the first spot. The measurements were extended over a period of several months. The average velocities at the first profile are summarized by GEIGER (1950, 1961) in the curves of Fig. 3. It is seen, that average wind velocities before leafing were about 1.25 m/sec in the typical trunk space and gradually increased through the crown space to the velocities above the forest. With the trees in full leaf the average velocity in the trunk space was 0.75 m/sec. Below 2 metres from the ground the wind velocities decreased rapidly. Wind velocities in the trunk space at the second profile with a dense undergrowth were 60–70 % of those at the first profile. Other measurements of air velocities in the trunk space are 1.5–2 m/sec by REMPE (1937) in a large alder stand before leafing. At free wind velocities of only 1.5–2 m/sec ZENTGRAF (1952) found 0.15–0.28 m/sec in deciduous forests in full leaf and with rather dense undergrowth. PFEIFFER (1938) measured velocities of 1.1 m/sec for the wind coming out from a spruce forest having a well developed trunk space, and NÄGELI (1953) found velocities of 0.7 m/sec in the trunk space of a coniferous forest dominated by spruce (measurements were taken only 1.4 metre above the ground with a free wind velocity of 6 m/sec).

The deciduous forests of the Atlantic period are often thought of as high, dark forests with little undergrowth except in scattered areas of regeneration, where the fall of dead trees had created openings in the canopy. These forests

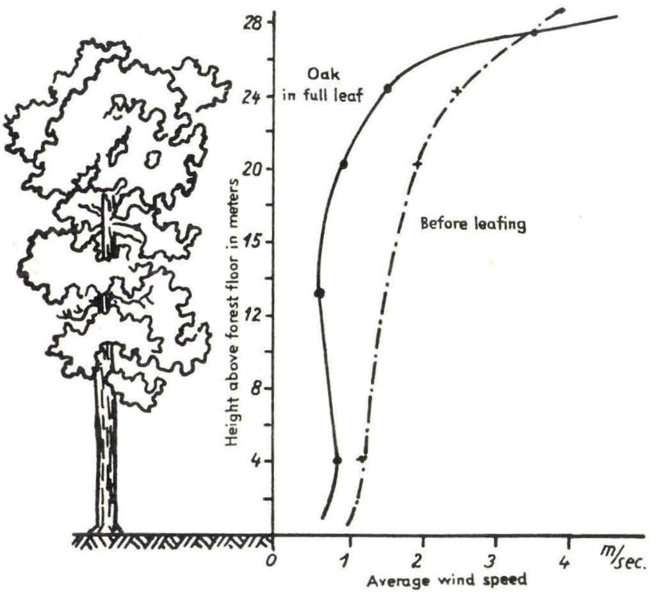

Fig. 3. Average wind velocities measured in an oak forest by Geiger and Amann (from GEIGER, 1950).

probably had a well developed trunk space and a good deal more openings in the canopy than modern, cultivated forests, in which the trees forming the canopy tend to be of the same age over large areas. Only the shore or border vegetation may in specific cases have formed a more serious obstruction to the wind flow in the trunk space. Forests similar to the Atlantic forests can hardly be found to-day. Of those mentioned above the oak forest where Geiger and Amann made their measurements is probably the one that resembles an Atlantic forest most, although it is likely that its underwood was somewhat denser. The measurements in Fig. 3 are therefore likely to give lower values than the expectable wind velocities in the trunk space of the Atlantic forests.

When these results are applied to pollen analysis, it should be remembered, that pollen of hazel, alder, aspen, elm, and certain species of willow are emitted before the trees come into leaf, while beech, oak, birch, ash, and maple flower either right before or simultaneously with the leafing when the canopy is not really closed. Of the large deciduous forest trees only lime (which is insect-pollinated) flowers in July when wind currents in the trunk space are suppressed. For the group of species that flower before leafing, wind velocities in the trunk space of Atlantic forests of 1–1.5 m/sec may be assumed, for species flowering simultaneously with the leafing velocities may be close to 1 m/sec, and for lime rather 0.5–1 m/sec. These velocities are thought of as average values in cases with no special obstruction to the flow in the trunk space; they may be modified by topography.

Wind currents in a forest may also be produced by cold air sinking from the crowns or moving downwards on slopes during evenings and nights with a strong radiation from the ground and from trees (KOCH, 1934; PFEIFFER, 1938). These currents are, however, restricted to times when the pollen concentration of the air is low, and their importance for the pollen transport is probably not great.

The amount of pollen in the trunk space relative to that above the crowns has been measured by REMPE (1937) in an extended alder stand. The trunk space was 9 metres high, and the anthers were scattered in the crowns from 9 to 13 metres above the ground. Alder pollen was collected with vertical cylinders having a diameter of 14 mm and covered with an adhesive on the surface. The cylinders were exposed at heights from 2 to 18.7 metres (i. e. up to 5–6 metres above the crowns). The wind velocity at 2 metres above the ground was 1.5–2 m/sec; based on the measurements by Geiger wind velocities at greater heights were estimated by Rempe to 2 m/sec up to 12 metres, to 2.5 m/sec at the top of the crowns, to 4 m/sec at 16 metres, and to 5.5 m/sec at 18.7 metres. Four pollen profiles, each extending over 2½ hour, were measured.

From these investigations Rempe concluded that the pollen drift (the number of pollen grains passing through a unit area during a given time) increased greatly above the crowns compared to that in the crowns and decreased rapidly with distance downward in the trunk space. However, Rempe did not know that the collection efficiency of a vertical cylinder in an air stream is highly dependent on both the weight of the airborne particles and on wind velocity (see chapter 3). If Rempe's measurements are corrected for different collection efficiencies using the wind velocities estimated by him, the results will be as shown in Fig. 4. It is seen that maximum values for pollen drift, as would be expected, are found in the crowns (i. e. at the place of emission), while the pollen drift decreases both upwards and downwards. At the same distance from the crowns the pollen drift was roughly 50 per cent higher in the trunk space than above the crowns. Rempe also measured pollen profiles in a beech stand and a hazel stand; the results are mentioned as similar to those above, but no figures are given.

The pollen drift p_d (corrected for collection efficiency) is proportional to the product of the mean wind velocity u and the pollen concentration p_c in the air

$$p_d = k\,u\,p_c \tag{8}$$

k being a constant which depends on the units in which p_d, u, and p_c are measured. Since the mean wind velocities estimated by Rempe were twice as high in the first 5 metres above the crowns as in the first 5 metres below the crowns, it follows from (8) that, in the specific case measured by Rempe, the pollen concentrations in the upper 5 metres of the trunk space were roughly three times as high as the pollen concentrations in the first 5 metres above the crowns.

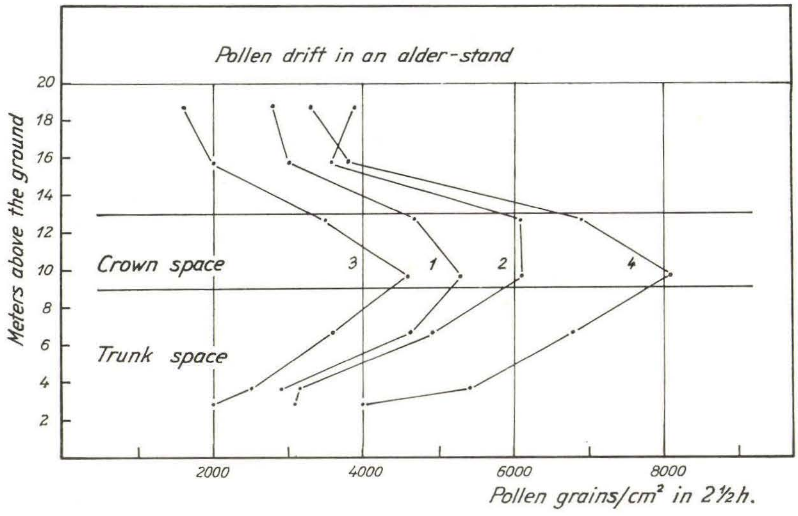

Fig. 4. Pollen drift in and above an alder stand measured by Rempe (1937); here corrected for varying collection efficiences using the wind velocities estimated by Rempe. Curve 1 was taken in the morning, curve 2 at noon, and curve 3 in the afternoon on the same day. Curve 4 represents measurements taken two days later.

Alder sheds its pollen very early in the year, and it is likely that pollen concentrations above the crown will be higher relative to concentrations in the upper part of the trunk space of pollen emitted later in the year. Still, it is obvious that large pollen concentrations will be present in the trunk space, and considerable quantities of pollen may be carried out of the forest by the wind currents passing here.

The formulae given in section 2.1. do not apply to dispersion within the trunk space. The warmest layer in a forest is usually the crown layer, the trunk space will therefore be characterized by a temperature inversion and turbulence will be suppresed. A rough estimate of dispersion distances in the trunk space may, however, be obtained by calculating the hypothetical trajectories which would be followed if the movement of the pollen grains were determined by wind velocity and terminal velocity alone. If released at a height of 20 metres small pollen grains with a terminal velocity of 2 cm/sec would in this case use 1000 seconds for the fall, and with a wind velocity in the trunk space of about 1 m/sec would during that time be carried a distance of 1000 metres horizontally. A beech pollen grain with a terminal velocity of 6 cm/sec would fall three times as fast and would therefore only be transported about 300 metres horizontally. These estimates lead to dispersion distances of the order of a few hundred metres and up to about thousand metres, different for each species. Small pollen grains emitted early in the year (e. g. of alder and hazel) when wind velocities in the trunk space are comparatively high will thus be dispersed over much longer distances in the trunk space than large pollen grains emitted later in the year (e. g. of beech and lime).

At heights below two metres wind velocities in a forest rapidly decrease to zero. Pollen emitted below that height will therefore be dispersed very badly, perhaps only over some tens of metres. Non-arboreal pollen deposited in lakes surrounded by closed deciduous forests can therefore only be expected to reflect ecological conditions at the forest edge and in the littoral zones.

The dispersion distances estimated above agree well with some field experiences from closed deciduous forests. In a beech-dominated forest on Zealand, Denmark, JONASSEN (1950) compared pollen spectra of moss polsters in the forest, and of mud samples from small lakes and ponds in minor glades, with the composition of the surrounding forest. Since large areas with spruce situated close to the beech forest yielded very little pollen in these samples JONASSEN (l. c., p. 58) concluded: "The local character of the spectra is, therefore, very particularly marked. For the greatest part, the pollen must originate from the forest inside a limit of a few hundred metres from the spot. It is, therefore, not possible to determine the composition of the forest from a spectrum originating in a forest covered area, even at a distance of 400–500 metres away". The same local character of the pollen spectra was found by WOLTHERS (1956) in an investigation of the topmost gyttja layers from Lake Gribsø (200 by 600 metres), Zealand, which is girdled by deciduous forest out to a distance of 100–200 metres from the lake followed by spruce forests.

Experiences on dispersion distances like those of JONASSEN and of WOLTHERS are hardly explainable, unless it is assumed that most of the deposited pollen was carried thorugh the trunk space.

2.4. Dispersion above the canopy

During day-time wind velocities close above a forest will usually be in the range of 2–6 m/sec. Pollen emitted in the crown layer may be raised into these winds by frictional or convective turbulence in the crowns. With increasing altitude the wind speed approaches the velocity of the geostrophic wind, which averages about 4–10 m/sec, and pollen dispersed above the tree crowns may therefore be carried over wide distances before it is deposited. Dispersion distances in the atmosphere above the canopy also depend on the vertical temperature gradient and on surface roughness which determine the degree of turbulence (compare Fig. 1). Little is, however, known of the relative importance of pollen contributions from areas at varying distances from the point of collection. Below, estimates of this gradient of decrease with distance has been made for some ideal cases.

Measurements of daily and monthly variations in the meteorological parameters that define dispersion in the lower atmosphere are available from several atomic energy research stations (e. g. HOLLAND, 1953; BJERRUM MØLLER and

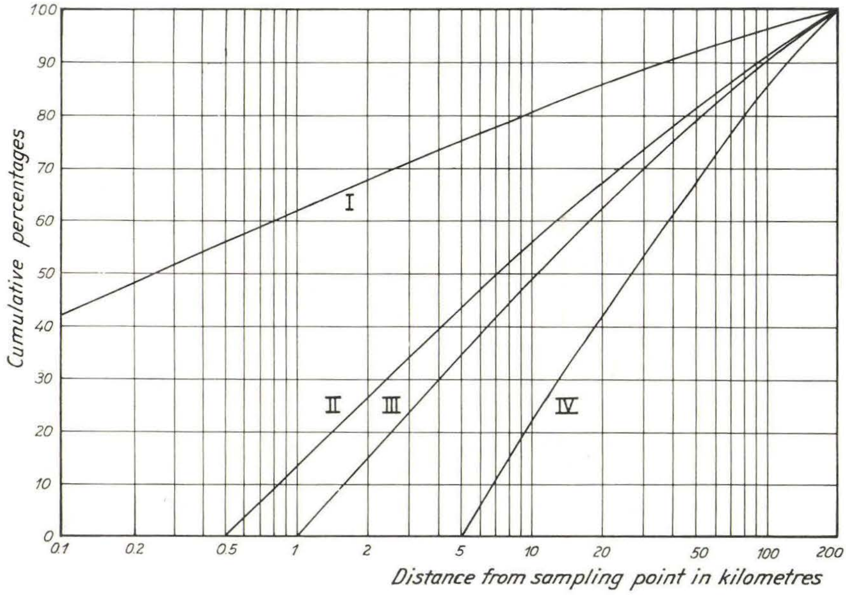

Fig. 5. The number of arboreal pollen grains coming from within a given distance from the sampling point expressed in percentages of the total number of pollen grains coming from within 200 km. Calculated for light pollen grains (terminal velocity 2 cm/sec) emitted under average meteorological conditions from an infinitely extended forest in a flat terrain. Only pollen carried above the canopy is considered. Curve I: pollen collected at a point immediately above the canopy; curve II, III, and IV: pollen collected 500 m, 1000 m, and 5000 m, respectively, in front of a forest edge. The curves show the strong gradient of decreased deposition with distance under average conditions.

JENSEN, 1959; JENSEN, 1962). With average wind velocities and neutral or slightly unstable lapse rates these parameters will have values close to the figures used in the calculation of the curves in Fig. 2 (section 2.1.). Applying these values, the relative number of pollen grains arriving from varying distances has been calculated for the case, where an infinitely extended forest is situated in flat terrain and is composed of species with an almost equal pollen production of either light pollen grains (terminal velocity about 2 cm/sec) or heavy pollen grains (terminal velocity about 6 cm/sec). In the calculations the crown layer is approximated to an infinite area source, and the number of pollen grains coming from belts between specified distances are found by integrating the contributions calculated from formula (5) between these distances. Before the integration a correction for deposition losses according to formula (7) was applied. If $h = 0$ is inserted in (5), the calculations will give the concentration of pollen grains at a height zero above the forest ,i e. immediately above the crowns. The results are expressed in Figs. 5 and 6 as cumulative percentages, i.e. as the number of pollen grains which has come from within a given distance relative to the total number of pollen grains present.

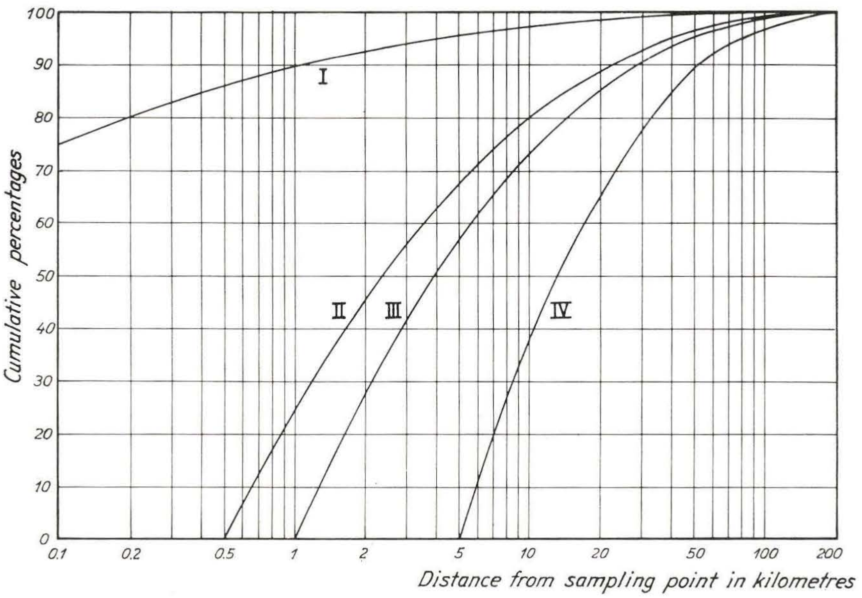

Fig. 6. A similar set of curves as in Fig. 5; here calculated for heavy pollen grains (terminal velocity 6 cm/sec). It is seen that the gradient of decreased deposition with distance is much steeper for heavy pollen grains than for light pollen grains.

The calculations have been extended to distances of 200 km, while pollen from beyond this limit has been disregarded. Sutton's formulae are not strictly applicable to such distances, and extrapolations beyond some kilometres will only give an order of magnitude. Errors arising in this way will, however, be suppressed when the results are expressed as cumultative percentages. Similar long-range extrapolations of Sutton's formulae out to a hundred kilometres have been made by U.S. Weather Bureau (1955) in estimates of dose rates from radioactive clouds, and by World Meteorological Organization (1960) in estimates of air pollution. In the latter paper account is taken of the fact that an inversion layer may sometimes be found at altitudes of 1–3 km. Such a layer will put a limit to the height in which vertical mixing takes place, and a somewhat different way of estimating was therefore proposed. For neutral or slightly unstable lapse rates, which characterize the average conditions assumed in the calculations, the two ways of estimating give very similar results.

Being rough estimates only, no account has been taken of the influence of the diurnal cycle in pollen emission, or of the effect of differences in dispersion distances at various times of the year. An uncertainty also arises from the fact that wind velocities on days of maximum pollen emission need not conform with the average velocities assumed in the estimates. If an important fraction of the pollen is shed on calm days with low wind velocities, the influence of long distance transport will be less pronounced than estimated here. Incidents of high wind velocities during the period of pollen emission will, on the other hand, increase the influence of long distance transport. Due to the aerodynamic roughness of a forest top and the trapping of pollen grains in the trunk space, the actual losses due to deposition will rather be greater than calculated here, but this may be counterbalanced by refloatation of pollen. Topographic obstructions to the transfer will, of course, favour local pollen.

The estimates for a forest composed of species with light pollen grains are given in Fig. 5. Curve I shows that 50% of the pollen present in a given volume close above the crowns have come from distances within 250 metres, 75% have come from within 5 km etc., while the number of pollen grains which comes, for instance, from distances between 5 and 10 km is of the order of 5% (80 minus 75%). The accuracy of these estimates should of course not be overrated, they give at best approximate magnitudes of the gradient of decrease with distance in cases resembling the ideal conditions assumed in the calculations.

While curve I indicates cumulative percentages directly above a forest, for instance at the forest edge, curves II, III, and IV in Fig. 5 give estimates of the corresponding percentages for light pollen grains at distances of 500 m, 1 km, and 5 km in front of a forest, respectively. Only the number of pollen grains which is transported above the forest is included in these estimates, since pollen in the trunk space is dispersed quite differently, as mentioned in section 2.3. The curves show that long distance transport constitutes proportionally greater fractions of the pollen from above the canopy the further away from the forest pollen is collected. Thus, according to these estimates, if collection is made 500 metres from a forest edge, roughly 50% of the pollen grains carried above the forest originate from distances greater than 7 km; at 1 km from a forest edge the 50% limit is roughly 10 km; and if pollen is collected 5 km from a forest 50% of the pollen grains from above the crowns will be expected to come from distances greater than 30 km. The marked influence of long distance transport in these cases is not due to more pollen grains coming from distant places, but to the abscence of the large quantity of pollen otherwise coming from the nearer parts of the forest.

Fig. 6 gives the same estimates for heavy pollen grains. The curves show that heavy pollen grains (e. g. beech pollen) are dispersed over much shorter distances. In this case 75% of the pollen in a given volume close above the crowns come from within 100 metres, 90% from within 1 km etc. The stronger dependence on distance for heavy pollen grains is caused by the larger losses due to deposition according to (7).

The estimates may for instance apply to pollen collected in the middle of a raised bog or in front of a forest margin, but only partly to pollen from a lake where mixing in the surface layers will obliterate the dependence on distance from the forest. The results of the estimates are in a reasonable agreement with experiences made in some of the classic investigations from raised bogs. Here it was found, that at times when the forest around a bog had been cleared, the pollen spectrum changed from a more local character to include substantial contributions from wide distances, as indicated for instance by secondary pine maxima (OVERBECK, 1928; STEINBERG, 1944). The importance of long distance transport relative to the number of pollen grains from the more near-by vegetation, as indicated by the curves, is also in a reasonable accordance with the experiences by AARIO (1940) on recent pollen deposition in North-Finland. AARIO found that large fractions of the pollen grains deposited on the tundra north of the forest limit originated from forest belts situated at great distances (50 km or more) to the south.

If the average values of the meteorological parameters deviate significantly from those assumed in the above estimates, pollen will be dispersed differently, and different gradients of decrease with distance will be found. This is likely to be the case for pollen emitted very early and late in the year, or in the warmest part of the year. The magnitude of the meteorological parameters will also vary with latitude. Species emitting their pollen in the warmest months (e. g. pine and lime) will at the same time have a larger fraction of their pollen lifted up above the crowns by convection currents and will in this way get a proportionally greater share in the long distance transport. The extent of the area which is effectively represented in the component carried above the canopy will therefore depend both on the terminal velocity of fall of the pollen grains, and on the time of pollen emission.

The estimates made above do not include the effect of anomalies in pollen dispersion due to large-scale weather phenomena connected for instance with the general circulation in the atmosphere, with the passage of front systems, thunderstorms, etc. Little is known of the relative importance of such phenomena on the total deposition. In a single case, the influence of turbulence associated with prefrontal instability was measured by BUELL (1947), who found about a doubling in deposition rate at a given distance from a pine forest during the passage. The difficulty is that in such cases both the dispersion pattern and the source strength, i. e. the number of pollen grains lifted up above the forest, vary at the same time. The additional deposition at different distances due to such instability is therefore difficult to estimate.

2.5. Rainout of pollen

Raindrops have diameters in the range of 0.2 to 4 mm and fall with terminal velocities of 1–10 m/sec, i. e. roughly 100 times as fast as the common pollen grains. Falling raindrops will catch pollen grains in the atmosphere by impaction and bring them to the ground (see section 3.3.). Pollen grains may also be trapped in the clouds and thus be present in the drops before precipitation. In the following no distinction will be made between these two ways of trapping, and the term "rainout" is used for all pollen grains brought down by rain, irrespective of method.

Due to the scavenging action of raindrops the air below cloud bases will be almost cleaned of pollen grains during the fall of one or a few millimetres of rain. At the same time the release of pollen from the near-by vegetation will stop. The concentration of pollen grains in the air therefore drops rapidly during the first part of a shower, while, in the case of prolonged raining, comparatively little is brought down during the subsequent period of rain. This has been shown by direct measurements of pollen concentrations in the air before and after periods of rain (REMPE, 1937, p. 126; HIRST, 1953). In the measurements by Hirst pollen concentrations above a grass field in July were determined with a volumetric spore trap before and during a thunderstorm. In the first half hour, in which 1 mm of rain was falling, the concentration of pollen grains in the air fell to $\frac{1}{6}$ of the concentration before the beginning of the thunderstorm. During the next 18 hours, in which 3 mm of rain came down, the air concentration decreased almost to zero.

Pollen brought down by rain will reflect the average spectrum in the cloud and in the entire air layer below cloud bases, i. e. in a column which will usually be about 0.5 to 3 km high. The origin of pollen in the layers close to the ground has been discussed in the preceding sections. At higher altitudes the influence of long distance transport will be very pronounced due to the high wind velocities in these layers and the time it takes for pollen to be carried into these altitudes. Under average conditions with neutral or stable lapse rates, the pollen concentration in the air decreases rapidly with height, and comparatively small amounts of pollen will be present in altitudes above a few hundred metres. In a number of meteorological cases including those which favour pollen emission the decrease with height is, however, only slight up to a 1000 metres or more as shown by REMPE (1937). This will be so for instance in cases of strong updraughts under cumulus clouds, or of strong thermal convection where an elevated inversion layer sets an upper limit to vertical diffusion. It may be noted that not only wind velocity but also wind direction at a few hundred metres above the ground will differ from the one at ground level, the wind in the lower layers being deflected due to surface friction. In flat terrain this deflection may average 25°. Pollen carried at different levels will therefore represent different areas both as to distance and to direction. But at any rate it is obvious that the rainout component will be the most regional of the three components considered here.

Only if rainout of pollen makes up a large fraction of the total pollen deposition in small lakes and bogs, will pollen diagrams from these basins be of a regional character. The ratio of rainout to dry deposition is therefore of great importance for the understanding of pollen diagrams. Unfortunately this ratio has never been directly measured and only very crude estimates can be inferred from published data.

REMPE (1937) collected pollen during a thunderstorm lasting for 4 minutes in May 1935. The pollen grains were caught in a glass on the roof of the Botanical Institute of Göttingen, i. e. in a garden area at the outskirts of a town situated in a fairly well forested area. One hour before the thunderstorm an ascent by airplane had shown that the atmospheric concentration of pollen grains was very high near the ground and considerable at least up to 500 metres above the ground. During the four minutes about 0.5 mm of rain was falling, and 4 pollen grains per cm^2 and per mm of rain was collected. Whether this figure is typical for the average number of pollen grains brought down per cm^2 and per mm of rain in a forested area during the season of pollen emission is difficult to say. Being the first 0.5 mm of rain falling on a warm day with a high atmospheric concentration of pollen grains one would expect the figure to be several times the average value for more prolonged raining. On the other hand, the near-by town of Göttingen will have reduced the number of pollen grains in the atmosphere compared to that of an entirely forested area.

In another experiment by GREGORY, HIRST, and LAST (HIRST, 1959; GREGORY, 1961) two conical funnels were exposed at a height of 2 metres above a grass field at Rothamsted Experimental Station, England. One funnel was open to rain (rain-trap), while the other (dry-trap) was protected by a flat roof held 25 cm above the mouth of the funnel to keep rain off but still allow dry deposition. Spores and pollen grains (mainly of grasses and weeds) were collected in both traps from June to September, 1951. It is worth noting that on dry days the fully exposed rain-trap consistently caught fewer pollen grains than the dry-trap with the roof, while the opposite was the case when raining. On an average, the number of pollen grains caught in the open rain-trap in dry weather amounted to only 80% of the number caught in the roofed trap. This is another proof that pollen grains are not falling like a "rain", but are moving in a predominantly horizontal direction.

During a thunderstorm beginning at 13.25 hours on July 22., 1951, and with rain lasting for 19 hours spores and pollen grains were collected in both funnels. The thunderstorm was the end of a 7-day spell of warm, dry weather. Half an hour before the beginning of the rain the concentration of pollen grains in the air near the ground was found to be as high as 750 pollen grains per m^3 of air (HIRST, 1953). As mentioned above this concentration fell to $\frac{1}{6}$ during the first half hour of rain. During the 19 hours of rain, in which 4.75 mm was falling, a surplus of 7 pollen grains per cm^2 and per mm of rain was collected in the open rain-trap above the number caught in the roofed trap. In the first half hour which gave 0.95 mm of rain the number of pollen grains collected in the rain-trap per cm^2 and per mm of rain was 5–6 times as high as the average for all 19 hours. It is not known whether the number of pollen grains deposited during this thunderstorm is typical for rainy periods during the period of growth. Although the agreement with the figure obtained by Rempe is fair, it is doubtful whether pollen production over an extended grass field and in a forested area are comparable. At the moment, however, these are the only published measurements on which an estimate can be based.

The total pollen deposition per cm^2 during the month of May was measured in Göttingen to 18,000 pollen grains. The measurement was made on the same roof where the rain sample was collected. The total deposition for the full year can therefore hardly be less than 20,000 to 25,000 pollen grains per cm^2 (the emission of pine pollen for instance was not finished). If we take the figure of 4 pollen grains per cm^2 and per mm of rain, assume about 300 mm of rain during the period of pollen emission, and a total yearly pollen deposition of 20,000 to 25,000 pollen grains per cm^2, rainout will amount to 5–6% of the total pollen deposition. If we assume a rainout of 7 pollen grains per cm^2 and per mm of rain, and the same total pollen deposition, rainout will equal 9–10%. In view of the uncertainties in the above assumptions the safest estimate at the moment is that rainout will be of the order of 10% in small lakes and bogs in fully forested areas and possibly somewhat more in the middle of big lakes and bogs where the total yearly dry deposition is expected to be lower.

It is obvious that the above estimate is very crude, and that actual measurements of this important quantity should be made thoughout a full period of growth in many different localities and under different climatic and vegetational conditions. It should also be realized that the ratio of rainout to dry deposition is likely to vary for different species. Those shedding their pollen in June and July, when dispersion through the trunk space is slowed down, and when large-scale convection is frequent, will thus be expected to have a ratio of rainout to dry deposition above the average.

2.6. The composite deposition

According to the analysis in the preceding sections the deposition of pollen grains in lakes and bogs surrounded by closed deciduous forests consists of three main components, the trunk space component (c_t), the component carried above the canopy (c_c), and the rainout component (c_r). Though to some extent interrelated, the three components will have essentially different origins, and therefore, in most cases, also different pollen spectra.

The division of pollen deposition into three components is illustrated in Fig. 7. Of the total number of pollen grains deposited per cm^2 the fraction transferred through the trunk space is called f_t, the fraction which has been carried above the canopy is called f_c, and the fraction brought down by rain f_r. If no other addition of pollen grains takes place, then

$$f_t + f_c + f_r = 1 \tag{9}$$

If the pollen percentage of a certain species (i) in component c_t is denoted $(p_i)_t$, and in components c_c and c_r $(p_i)_c$ and $(p_i)_r$ respectively, then the pollen percentage p_i of that species in the total deposition is

$$p_i = (p_i)_t\, f_t + (p_i)_c\, f_c + (p_i)_r\, f_r \tag{10}$$

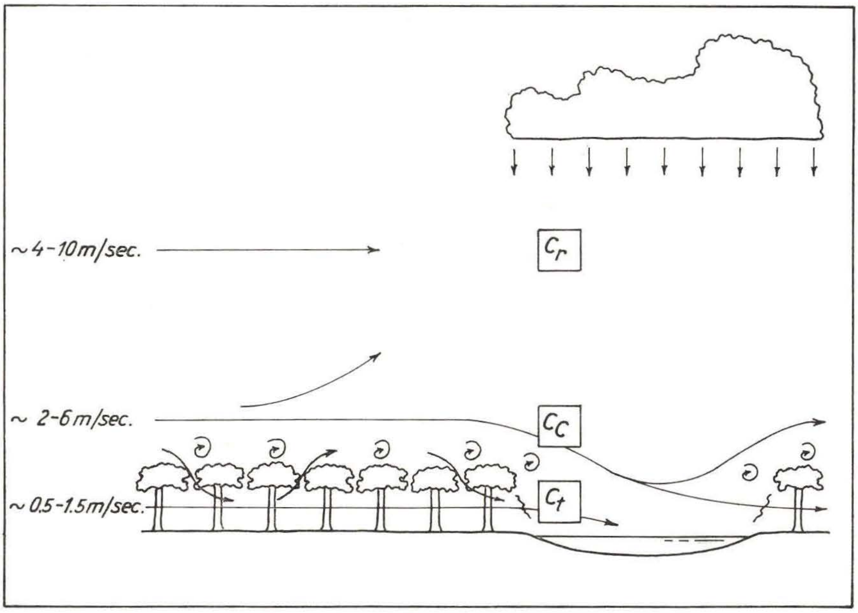

Fig. 7. Tentative model of pollen transfer in a forested area.

Due to the different origin of the three components it is essential, in order to understand a pollen diagram, to know the respective share of each of the components in the total pollen deposition. These ratios are, however, not known at the moment. It will be one of the most important tasks in future pollen investigations to determine likely values for the factors f_t, f_c, and f_r in various vegetational and topographic cases, under different climatic conditions, and in basins of varying sizes. The factors are moreover, likely to be different for each species, even at the same locality, depending mainly on the size of the pollen grains and the time of the year when pollen is emitted.

It may be mentioned that it is possible that most or nearly all pollen grains of a certain species are present in one of the three components alone, for instance in the rainout component, i. e. that $(p_i)_t$ and $(p_i)_c$ are very small or zero, while $(p_i)_r$ is of a significant magnitude. If this is the case, changes in the pollen percentage of this species will not serve as an indicator of vegetational changes in the direct vicinity of the basin, and the changes in the curve of this species in the pollen diagram need not fit ecologically into the rest of the changes shown in the diagram.

As an intermediate stage before final sedimentation pollen may also be dispersed by watercourses and by the action of water currents. In the process of dispersion by streams a differential floatation and settling will take place (HOPKINS, 1950; MULLER, 1959). Coniferous pollen grains, in particular, will float for a long time on water surfaces due to the buoyancy of their air-sacs;

for this reason they also tend to accumulate in shore deposits in lakes as a result of the action of wind and surface currents. Settling velocities will vary with size and density of the pollen grains, in general the settling rates will correspond to those for fine silt fractions. Rivers may, moreover, carry a load of reworked material containing secondary pollen. In the above general treatment no account was taken of dispersion by water transportation. In cases where this is important formulae (9) and (10) may, however, easily be adapted to include a fraction f_w representing the waterborne component.

The importance of the factors f_t, f_c, and f_r may be illustrated by a rough evaluation of possible figures for the three factors in two extreme cases:

1) For the pollen deposition in the middle of a small lake or bog with a diameter of 100–200 metres approximate values for the three factors may be

$$f_t = 0.8$$
$$f_c = 0.1$$
$$f_r = 0.1$$

2) In the middle of a large lake or bog with a diameter of some kilometres the corresponding values are more likely to equal

$$f_t = 0.1$$
$$f_c = 0.7$$
$$f_r = 0.2$$

It is obvious that the pollen diagrams will have a very different character in the two cases. In the first about 80% of the pollen grains come from the trunk space and drastic filtration effects may occur through certain changes in the vegetation (see section 3.2.). In the second case the overwhelming part is carried above the canopy and filtration will be much reduced. The main difference will, however, be in the size of the area represented. In the first case the effective source area will extend to about 300–1000 metres from the basin depending on the species present. In the second case the effective source area may extend to a distance of the order of 30–100 km from the basin. In these estimates the "effective area" is taken as the area from which 80% of all the pollen grains originate. The area represented in a pollen diagram thus depends very strongly on the degree of forest cover and on the size of the basin. This explains the fact that evidence for both very local diagrams (JONASSEN, 1950; WOLTHERS, 1956; SMITH, 1961) and for very regional diagrams (OVERBECK, 1928; AARIO 1940; STEINBERG, 1944; DAVIS and GOODLETT, 1960) can be found in pollen analytical literature.

Variations in the extent of the area represented may also occur at different levels in the diagram from a single locality, if the denseness of the forest cover changes through the time period covered by the diagram. This applies especially to the transition from the Boreal to the Atlantic period in which the deciduous forest cover became closed, and to later periods of deforestation by man. In these cases the changes shown in the diagrams will not be due to vegetational changes with time alone, but also to variations in the size of the area represented in the diagram. A striking example of the change from a local to a regional character of a diagram can be found for instance in the investigations of the bog Rote Moor (OVERBECK, 1928). A clearing of the forest around the bog in medieval times showed up in the diagram as a transition from a beech maximum to a pine maximum. High beech pollen percentages (30–60%) in a small or medium sized lake or bog surrounded by forests indicate that beech trees were growing close to the basin and dominated within the first half kilometre (but not that beech was dominating in the whole region). The high pine percentages that followed after the clearing of the nearest beech forest show that the diagram changed character and now reflected the vegetation within a much larger area.

The composite nature of pollen deposition, which results in great differences in the extent of the area represented and in varying gradients of decreased deposition with distance, is probably the main reason for the large and varying inconsistencies which are found in comparisons between pollen percentages and the frequencies of species in the surrounding vegetation (e. g. STEINBERG, 1944; JONASSEN, 1950; POTZGER *et al.*, 1956; POTTER and ROWLEY, 1960; DAVIS and GOODLETT, 1960). Another reason is of course the varying pollen production of different species. No simple relation between pollen percentages in a deposit and frequencies of species (or pollen production of species) can therefore be expected. It should also be remembered that many anomalies in dispersion may occur in specific cases due to minor eddies and to local variations in wind direction and wind velocity caused by topography and by varying degrees of aerodynamic roughness of the vegetation. The description of pollen dispersion given above should therefore only be taken as a broad generalized picture of the processes which are likely to dominate dispersion in and around a forest.

3. DIFFERENTIAL POLLEN FILTRATION

3.1. Impaction of airborne particles on obstacles

Air currents bend around obstacles (e. g. branches) encountered on their way. Particles carried by the wind tend to follow the air stream around the obstacle. However, due to the inertia of the particles their trajectories will deviate from the streamlines of the air and may intersect with the surface of the obstacle. In this way a fraction of the particles will strike the obstacle and may adhere to it. This is illustrated in Fig. 8.

The fraction of the particles which are captured by impaction on an obstacle is measured by the so-called collection efficiency E. This is the ratio of the number of particles collected by the obstacle to those which would have passed through the area taken up by the obstacle if it had not been there. The greater the collection efficiency the greater will be the number of particles caught by the obstacle.

Collection efficiencies have been studied extensively both theoretically and

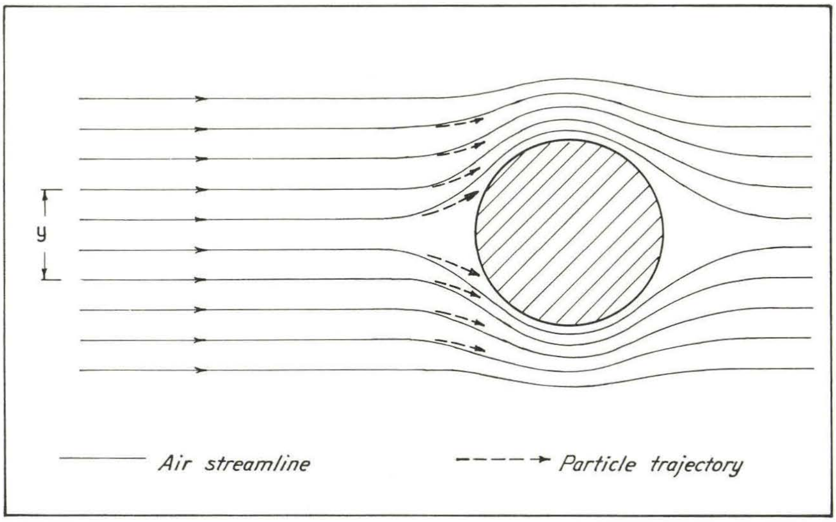

Fig. 8. Capture of airborne particles on a cylindrical obstacle in the case of streamline motion. Particles within the section y will strike the obstacle, while particles outside that section will be carried around the obstacle.

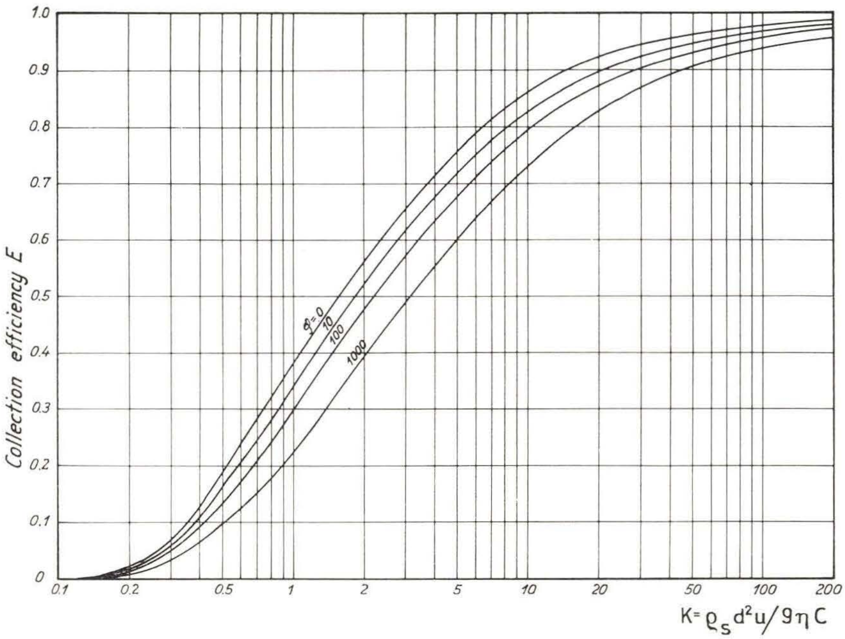

Fig. 9. Collection efficiencies according to LANGMUIR and BLODGETT (1945).

experimentally because of their great importance for dust collection, icing of aeroplanes, etc. (LANGMUIR and BLODGETT, 1945; RANZ and WONG, 1952; WONG, RANZ, and JOHNSTONE, 1955; DAVIES and PEETZ, 1956; GREGORY, 1951 and 1961). It has been found that E for inertial impaction on cylinders is a function of the dimensionless quantities

$$K = \frac{1}{9} \frac{\rho_s d^2 u}{\eta C} \tag{11}$$

and

$$\varphi = 9 \frac{\rho_a{}^2 C u}{\eta \rho_s} \tag{12}$$

Here ρ_s is the density of the airborne particle (g/cm^3), d is the diameter of the particle (cm), u is wind velocity (cm/sec), η is the viscosity of air (1.77 10^{-4} g/cm sec at 15°C), C is the diameter of the collecting cylinder (cm), and ρ_a is the density of air (g/cm^3).

Curves of E against K for various values of φ have been calculated by several authors. The efficiencies given by LANGMUIR and BLODGETT (1945) for collection on cylinders at φ values equal to 0, 10, 100, and 1000 are shown in Fig. 9. These collection efficiencies have been tested experimentally, for instance for dust particles (RANZ and WONG, 1952; WONG, RANZ and JOHNSTONE, 1955) and for *Lycopodium* spores having diameters of 32 μ (GREGORY, 1951, 1961). The agreement with theory was good. Similar curves have been calculated for the collection on spheres and ribbons. The efficiencies are computed for spherical particles, and minor variations in collection efficiencies may occur for particles having other shapes.

It follows from (11) and (12) and the curves in Fig. 9 that E increases rapidly with the size and mass of the airborne particles and with wind velocity, while it decreases with increasing diameter of the cylindrical obstacle. Thus, if collected on a cylinder with a diameter of 0.8 cm and in a wind of 1 m/sec, E for birch pollen grains ($d = 21\ \mu$, $\rho_s = 1$ g/cm^3) is 0.09, while for beech pollen grains ($d = 42\ \mu$, $\rho_s = 1$ g/cm^3) under the same conditions E is 0.46, i. e. five times as high. Large distortions will therefore occur when cylinders covered with an adhesive are used for collection of pollen grains from the air. If for example the air contains 50% birch pollen grains and 50% beech pollen grains, the percentages of the pollen grains caught on the cylinder under the above mentioned conditions will be 16% birch pollen and 84% beech pollen.

If the wind velocity had been 2 m/sec instead of 1 m/sec, then the collection efficiencies for birch pollen and beech pollen on the same cylinder would have been 0.24 and 0.61, respectively, and the percentages of the pollen grains caught would therefore have been 28% birch pollen and 72% beech pollen. At the same time the total number of pollen grains captured on the cylinder would have been 55% higher than in the first case.

Collection of pollen grains by impaction on sticky cylinders and slides has been widely used in pollen investigations. Yet it is obvious from the preceding example that all results on pollen drift and pollen percentages obtained in this way must be corrected for varying collection efficiencies. This applies for example to the comprehensive and fundamental investigations by REMPE (1937). Both his figures for pollen production, pollen drift in and above the vegetation, and for the decrease of pollen concentration with height need corrections. Only if the impaction takes place at velocities great enough so that collection efficiencies approach 1 for all species can a correction be avoided. This is the case with the roto-rod and the roto-bar samplers (SHELDON and HEWSON, 1959) in which a small bar covered with an adhesive is rotated through the air with a high, constant speed.

The capture of pollen grains on branches will be similar to the collection on vertical cylinders, and capture on leaves will resemble the collection on ribbons. Collection efficiencies of leaves are, however, rather uncertain, since a large proportion of leaf surfaces are horizontal, and since leaves tend to move in the wind so that the surface exposed to impaction by airborne particles becomes smaller.

According to LANGMUIR and BLODGETT (l. c.) the collection efficiency will be zero for $K < 0.125$, i. e. in such cases the particles will be carried around the obstacle without any impaction taking place. For a cylinder with a diameter of 1 cm this will happen for birch pollen at wind velocities below 0.45 m/sec, and for beech pollen at wind velocities below 0.1 m/sec. Conversely, with a wind speed of 1 m/sec collection of birch pollen becomes zero if the diameter of the cylinder is greater than 2.2 cm, while at this wind velocity the collection of beech pollen stops for cylinders having diameters greater than 9 cm. Tree trunks will therefore only catch pollen grains at higher wind velocities, and the main part of the collection will take place on minor branches and on leaves.

3.2. Filtration of pollen grains in the vegetation

When pollen grains are carried through the vegetation a fraction of them will be caught on branches and leaves as described in the preceding section. Consequently, the air itself will be depleted of pollen grains, and preferentially of heavy pollen grains. The degree of filtration will depend on the average diameter of the branches and the size of the leaves, on the velocity of the air currents in the vegetation, and the denseness and the depth of the vegetation. In order to get a quantitative estimate of the filtration effect, it is therefore necessary to obtain a measure of the denseness of that part of the vegetation which acts as a filter. This can be accomplished by introducing a quantity δ, called the collection depth or the cross section depth (JOHNSTONE *et al.*, 1949). This is the horizontal distance through the filtering vegetation for which the sum of all the vertical sections of the branches and the leaves is equal to the vertical section of the whole filtering vegetation (see Fig. 10).

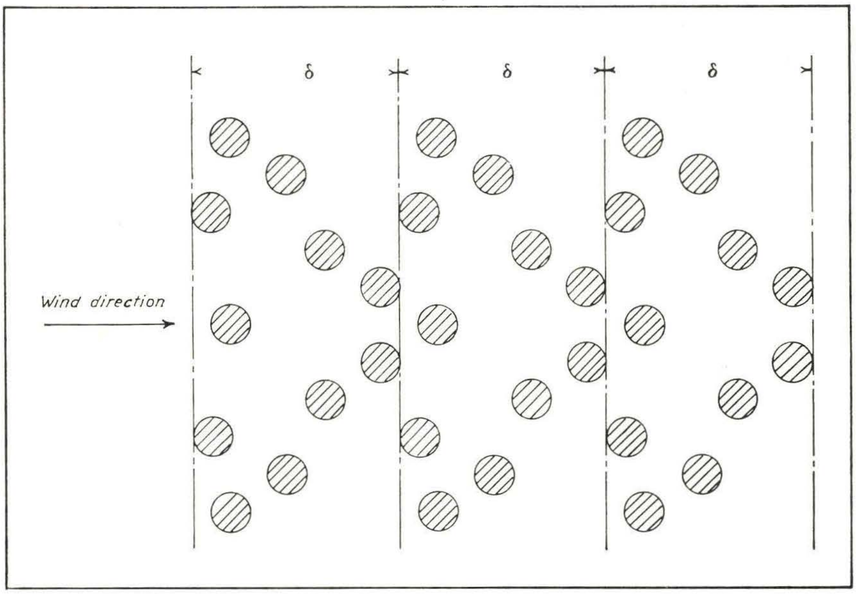

Fig. 10. Schematic illustration of the concept of collection depths δ. The drawing shows a horizontal section through a system of vertical branches.

Now, if the collection efficiency of the vegetation for pollen grains of a certain species is E, and if streamline motion is assumed, then the fraction of the pollen grains of that species which will remain airborne after the passage of a distance δ is (l–E). After the passage of n collection depths the airborne fraction relative to the number before the filtration will be

$$f = (1-E)^n \qquad , n = 1, 2, 3, \ldots \tag{13}$$

If the depth of the filtering vegetation is only a fraction of δ, an approximate formula will be

$$f = 1-nE \qquad , 0 < n < 1 \tag{14}$$

In the calculation of E the average thickness of the filtering elements and the average wind velocity in the vegetation may be used provided that the variations are not too large. Due to the irregular nature of shrub vegetation and of a canopy, δ and n will not be known with any high accuracy, and the fractions calculated according to (13) and (14) will only give an approximate magnitude of the filtration effect. Still, such an estimate may prove useful.

A similar theory has been advanced and partly tested for the penetration of insecticidal aerosols through a forest canopy (JOHNSTONE *et al.*, 1949; BURNETT and THOMPSON, 1956).

An example will show the importance of filtration in the vegetation. Let us again assume that the air contains 50% birch pollen grains and 50% beech pollen grains. It is further assumed that air with these pollen concentrations passes with an average velocity of 1 m/sec through a shrub vegetation having a depth of 2 δ and an average thickness of the branches of 0.8 cm. The percentages in the air at the exit from the shrubs can then be calculated from (13) when it is remembered that under these conditions $E = 0.09$ for birch pollen grains and $E = 0.46$ for beech pollen grains (see section 3.1.). The fraction of the birch pollen grains that remain airborne after passage through the shrubs is $f = (1 - 0.09)^2 = 0.83$, while for beech pollen $f = (1 - 0.46)^2 = 0.29$. Under the assumed conditions only 17% of the birch pollen grains will thus be captured in the vegetation, while 71% of the beech pollen grains will be lost. After filtration the percentages in the air will therefore be 74% birch pollen and 26% beech pollen.

A certain filtration will always take place during the passage through the trunk space and the vegetation at the forest edge. The effect will, however, be much greater if an additional filtering element in the form of a high shrub vegetation grows up along the shore of a lake or at the border of a bog, e. g. due to a desiccation of the basin. Such a belt of shrubs will act as a filter to most of the pollen grains carried in the trunk space. The effect may therefore be very drastic in small lakes and bogs where the trunk space component is considered to dominate the pollen deposition. In this case a sudden deflection of all pollen curves may result, even in the absence of significant changes in the pollen production of the surrounding species. The filtration effect will be easier to recognize if the shrub vegetation itself only produce a small amount of pollen relative to the total pollen deposition in the basin. An example of the calculation of pollen filtration in a case like this is given in chapter 4.

The species most likely to form a shrub vegetation at the border of lakes and bogs are willow (e. g. *Salix cinerea*), alder (*Alnus glutinosa*), and birch (*Betula pubescens*). Of these willow may be the densest due to the large number of thin branches developed. For full grown shrubs of *Salix cinerea* the collection depth δ will only be about 4–5 metres before leafing and somewhat less after leafing. Moreover, the young branches on *Salix cinerea*, which are most efficient as pollen collectors, are covered by fine hairs that will retain pollen grains very effectively after capture. *Betula pubescens* also has hairy branches, while the young branches on *Alnus glutinosa* are sticky. All three species are therefore excellent pollen collectors likely to retain all pollen grains that hit the branches even at high wind velocity where a certain refloatation may otherwise occur. Heavy rain will probably wash off the pollen grains and deposit them on the ground underneath the shrubs. In this way the branches are restored as pollen collectors. In most cases δ will be larger for alder and for birch than for willow, perhaps 10–30 metres before leafing. A rough idea of the magnitude of the collection depth can be obtained from the distance necessary to conceal a visible object, i. e. the distance through the shrub that may just not be penetrated by rays of light.

A shrub vegetation around a basin will at the same time act as a shelterbelt and reduce wind velocities in the trunk space. The area represented in the trunk space component will therefore be reduced, and heavy pollen grains and pollen from species growing at comparatively long distances from the basin will be most affected. In nature the shelter and the filter effect will occur simultaneously, and it may not always be easy to decide which will be the dominating one. It is thus possible that a filtering of pollen will dominate before the shrubs are in leaf and the wind velocities in the trunk space are higher, while a sheltering effect may be prevalent when the foliage is fully developed. At any rate, both effects will considerably reduce the total pollen deposition in small basins.

Differential pollen filtration has never been taken into account in pollen analysis and has not yet been established in field investigations. Two examples of filtration of pollen grains in the vegetation are, however, given in the literature. DENGLER (1955) measured concentrations of pine pollen in the trunk space of stands of different species. The pine pollen in the trunk space of these stands originated from distant sources. The measurements were made by sucking a known volume of air through a conimeter. The results should therefore be nearly independent of varying wind velocities in the trunk space. While the concentrations were comparatively constant in the trunk space of old stands irrespective of species, a significant lowering in the number of collected pollen grains was found when the air currents had to pass through young stands with a shrub-like character. JENSEN and BØGH (1942) found very pronounced reductions in the number of pollen grains caught behind hedgerows of different types relative to the number caught in front of the same hedgerows, the number of pollen grains behind the hedges being only a few per cent of the number caught in front of the hedges. Pollen was collected with glass slides (2.5 × 7.5 cm) placed vertically 1.0 to 1.25 m above the ground. The pollen sources were fields of ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*), and mangold (*Beta vulgaris subsp.*). Due to the relative lee behind a hedgerow the collection efficiencies of the slides are lower behind the hedge than in front of it. Unfortunately information on wind velocities is lacking and a correction can therefore not be made, but with usual reductions in wind velocities behind shelters this alone can hardly explain the drastic decrease in pollen capture. The measurements therefore suggest a combined filter and shelter effect, in which a part of the pollen grains in the first few metres above the ground is filtered off in the hedgerow and another part is lifted up above the hedge and deposited further away.

3.3. Rainout efficiencies

The capture of pollen grains by falling raindrops is a special case of collection by impaction. Raindrops fall through the air with velocities that are much greater than the terminal velocities of pollen grains (of the order of 100 times greater). Pollen grains will therefore be caught by raindrops with the same collection efficiencies as if they moved towards a sphere with a velocity equal to the difference between the sinking rates of the raindrops and the pollen grains. The collection efficiencies for this case has been calculated by LANGMUIR (1948). Due to the comparatively large relative velocities and the small size of the raindrops, collection efficiencies for pollen grains are high. Assuming a density 1 and a diameter of 20 μ for the pollen grains collection efficiencies of raindrops with diameters from 0.2 to 3 mm vary from 0.66 to 0.89; for pollen grains with diameters of 40 μ the corresponding efficiencies are 0.86 to 0.97. Minor deviations in collection efficiency may be caused by varying degrees of wettability of pollen grains (PEMBERTON, 1960; MCDONALD, 1964). This effect, however, does not seem to be great. Thus, pollen grains of lime, which have a coating of oil on the surface, are washed out of the air as effectively as other pollen grains (DINGLE and GATZ, 1963).

The rate of removal of pollen grains from the air further depends on the distribution of raindrop sizes in the particular type of rain, and on the amount of rain falling. Calculations show that the fall of a few millimetres of rain will clean the air almost totally of all types of pollen grains (CHAMBERLAIN, 1955; MCDONALD, 1962). This has also been found in field investigations (REMPE, 1937; HIRST, 1953; MAY, 1958; DINGLE and GATZ, 1963).

In light rain showers where only a fraction of the airborne pollen grains is brought down, rainout of pollen will to some extent be differential giving an enrichment of heavy pollen grains relative to the concentrations in the air. For larger showers and prolonged raining the removal will approach 100% for all types of pollen grains. The total rainout of pollen will therefore only be slightly differential for different species.

4. THE ATLANTIC/SUB-BOREAL TRANSITION IN THE VALLEY OF WEIER

4.1. Different versions of the Weier-diagram

In order to illustrate how the above theories of pollen dispersion and filtration may be applied in pollen analysis, parts of a diagram from a former lake at Weier are discussed below.

The Weier-valley is situated south of Thayngen in Switzerland. Topographically it is a small oblong valley surrounded on all sides by hills, 40–80 metres high, except for a narrow opening towards the Fulach-valley to the West. The long axis of the valley, which is directed mainly West-East, is a little less than 2 km, and the distance across, between the tops of the flanking hills, is only about 800 metres (compare map in TROELS-SMITH, 1955). In Atlantic and Sub-boreal time the valley contained a shallow lake, oval in shape, and hardly more than 100 by 500 metres. The lake had a small outlet to the river Fulach, but no inflow of water. With this isolated situation the trunk space component is likely to dominate, and it may be assumed that the fractions of the different components of the pollen deposition are about equal to those in case 1 in section 2.6.

A pollen diagram from Weier covering late Atlantic and early Sub-boreal time has previously been published and discussed by TROELS-SMITH (1955, 1960) in connection with investigations of lake or bog dwellings erected by Neolithic people on an islet in the Weier-lake. A new series of samples from an open profile in the central part of the former lake, 12 metres east of the islet, was collected in 1958 by J. TROELS-SMITH and SVEND JØRGENSEN. The samples were taken in a gyttja sediment with a vertical distance of only 2 cm between each. It is assumed in the following that the sediment constitutes a continuous series with no lacunas. The samples have been pollen analysed by SVEND JØRGENSEN; 2500 to 3500 pollen grains were counted in each. This new diagram shows a development which is parallel in all essentials to the previous diagram, and it has the advantage of covering a slightly longer time period.

With the permission of the collectors curves for some of the more important species in this diagram are shown in Plate 1. Calculations of the pollen percentages are based on the sum of all arboreal species including hazel (Σ AP). The most striking feature of the pollen diagram is the abrupt fall of the beech curve and the corresponding sudden rise of the curves for oak, hazel, birch, and willow above sample No. 14. After these drastic changes the curves remain nearly constant throughout six samples and then suddenly return to almost the same values as in sample No. 14. Dendrochronological investigations (HUBER and JAZEWITSCH, 1958) and radiocarbon dates (OESCHGER *et al.*, 1959; TAUBER, 1964, and unpublished) of construction timber from the lake dwellings suggest that the settling phases, which partly coincide with the period of the strong decrease in beech pollen, lasted for a rather short time interval, perhaps only one or two hundred years.

A relative pollen diagram like that in Plate 1 would usually be interpreted to indicate that the production of beech pollen declined abruptly after sample No. 14, while the pollen production of oak, hazel, birch, alder etc. increased. Before proceeding with the discussion of the Weier diagram the validity of such conclusions should be discussed.

In order to draw conclusions about changes in pollen production from a relative diagram, the following requirements should be met:

1. The total deposition of pollen of the species included in the pollen sum should be constant or nearly constant per cm^2 and per time unit throughout the period covered by the diagram.
2. The physical factors affecting dispersion, filtration, and deposition of pollen grains should be almost constant throughout the period considered.
3. The extent and the location of the effective source area should be nearly unchanged.

Re 1. A pollen curve for a species (i) in a relative diagram depicts (with a certain statistical accuracy) the ratio of the deposition d_i of pollen grains of that species to the deposition D_s of pollen grains of all species included in the pollen sum, versus depth in the sediment (i. e. d_i/D_s versus a non-linear time scale). If D_s has varied throughout the period considered, the ratio d_i/D_s may vary irrespective of changes in d_i. Only if D_s has remained constant or nearly constant, will the ratio d_i/D_s reflect the true variations in d_i. The species included in the pollen sum should therefore be chosen so that variations in D_s will be as small as possible. Yet, it is often difficult or impossible to check whether D_s has been constant throughout a diagram because the growth rate of the sediment may have varied at the same time.

Re 2. Variations in pollen deposition may be due both to variations in pollen production (caused by expansion or reduction in the area covered by species or by migration of species relative to the basin), and to variations in pollen dispersion and filtering. In stable periods with only moderate changes in the vegetation, variations in pollen production are likely to be the main cause of variations in deposition, though no simple relation can be expected between the magnitudes of the changes in pollen production and the resulting changes in deposition. In transitional periods with material changes in the structure of the vegetation this need not be the case, since the pattern of dispersion and filtration are likely to change at the same time. If this happens, pollen of different species will be affected differently depending on the size of the pollen grains, the time of the year when pollen is emitted, and the distance to the basin. In such periods the vegetational changes can therefore not be deduced directly from a relative pollen diagram. For the same reasons it is dangerous to use a pollen sum consisting of some selected species whose pollen deposition supposedly has varied greatly and to express the deposition d_i of another species relative to this sum. In transitional periods, where both D_s and the pattern of dispersion vary, it is very difficult to know whether a curve calculated in this way will reflect dissimilarities in dispersion and filtration, or variations in pollen production, or a combination of both effects. Various and variable rates of pollen production of different species may also obscur the picture of the actual changes taking place in transitional periods.

Re 3. A change in the total pollen deposition per unit area will usually be accompanied by a change in the extent of the effective source area. The smaller the deposition of pollen from the adjacent vegetation, the higher will be the percentages for pollen grains coming from great distances, and the larger the effective area represented. In a relative diagram the course of pollen curves for species growing at great distances will therefore, to a large extent, be determined by the degree of forest cover around the basin, by the denseness of the littoral vegetation, and by the expansion or reduction of nearby prolific pollen producers. The extent to which the effective source area may change also depends on the topography around the basin.

In Weier, where the trunk space component is thought to dominate, and where the littoral vegetation (alder and willow) seems to have changed greatly, both the total deposition of arboreal pollen grains and the dispersion and filtering are likely to have varied considerably throughout the period covered by the diagram. Only the extent of the effective source area may have been approximately constant because the topographical conditions around the basin to a large extent will prevent pollen grains from outside the valley from reaching the lake, except in the form of rainout. At least the first and the second of the above mentioned requirements are thus not likely to have been fulfilled for the Σ AP diagram from Weier. Consequently the diagram can not be expected to show the real variations in pollen deposition, nor will it indicate real variations in pollen production. An ecological interpretation of this diagram is therefore not warranted.

In order to get a safer basis for the discussion of the actual changes taking place, it is necessary to look for a quantity which is likely to have been more constant throughout the diagram than the deposition of pollen grains of all arboreal species, and to express the deposition of pollen of different species in units of this quantity. In the case of Weier the deposition of pine and spruce pollen may be used in this way. The reasons are the following:

The percentages of pine pollen and spruce pollen is approximately constant and very low up to sample No. 14, 0.7% and 0.1% of Σ AP respectively. Such low pine percentages are only rarely found in pollen diagrams, since pine pollen is produced in large quantities and is known to be dispersed very effectively. Pine and spruce are not natural constituents in an Atlantic forest under the edaphic and climatic conditions prevailing at Weier. The low percentages will therefore most probably mean that pine and spruce were not growing in the valley of Weier nor in the immediate vicinity. This is also consistent with the fact that macroscopic remains of all arboreal species represented in the pollen diagram, except pine and spruce, have been found in the culture layers from the lake dwellings in the valley (NEUWEILER, 1925; HUBER and JAZEWITSCH, 1958). Since the valley was surrounded by hills 40–80 metres high, i. e. with the canopy on the crests 60–100 metres above the lake surface, very little pollen from outside the valley would be carried down to the lake by the winds passing above the canopy. If growing outside the valley pine and spruce pollen will therefore almost exclusively have been brought dowh with rain. The deposition of pollen grains of these species will thus be expected to be independent of vegetational changes in the Weier-valley itself and therefore also of possible filtration effects in the littoral vegetation; the deposition will mainly have depended on the production of pine and spruce pollen within the source area and on possible changes in precipitation during the months of May and June. For these reasons the deposition of pine and spruce pollen is assumed to have been almost unchanged during the period considered, or at any rate to have been more constant than the total deposition of pollen from arboreal species. Pollen of fir (Abies) might have been included in the sum as well, since most of the arguments given above also apply to the deposition of pollen grains of this species. However, fir seems to have migrated into the valley at the end of the period considered, and the pollen deposition of that species is therefore likely to have varied.

The curves for the species shown in Plate 1 have been recalculated on the basis of a pollen sum consisting of Σ (Pinus + Picea). The new diagram is shown in Plate 2. For statistical reasons the curves in this diagram will be more choppy than those in the Σ AP diagram. Furthermore, during the drawing of the diagram it became clear that a number of peaks occurred in all curves at the same levels and therefore must be caused by fluctuations in Σ (Pinus + Picea). At these levels (sample Nos. 4, 11, 15, 19, and 21) smoothed-out values of the curves are indicated by dotted lines in addition to the original curves in full line.

The development of the curves in the two diagrams is parallel up to sample No. 14, but from sample No. 14 to sample No. 24 the course of the curves in the new diagram is very different from that in the Σ AP diagram. In this interval the beech curve falls still more abruptly in the Σ (Pinus + Picea) diagram, while the curves for oak, hazel, and birch which previously rose strongly show a slight fall in the new diagram. The curve for alder first decreases slightly and then show a strong rise; the willow curve is the only one that rises strongly during this interval and then partly returns.

If it is correct that the deposition of pine and spruce pollen has been approximately constant throughout the period covered by the diagram, then the first requirement mentioned above is fulfilled for the Σ (Pinus + Picea) diagram. This diagram will then show the absolute and real variations in pollen deposition in Weier lake, in the sense that a doubling in the values for a species in the diagram will reflect a doubling in the deposition per cm^2 and per time unit of pollen grains of that species in the lake. It may be noted that in a diagram like this, the fall in some of the curves need not be compensated for by a corresponding rise in other curves. The deposition of pollen grains may well decrease for all species at the same time. A curve showing the variations in the total deposition of pollen grains of all arboreal species is also drawn in the Σ (Pinus + Picea) diagram. This curve shows a slight decrease in deposition of pollen grains of arboreal species during the expansion of beech up to sample No. 14, as would be expected due to the low rate of pollen production of beech trees, and a sudden fall to about half of the previous deposition during the fall in the beech curve. Later a return like that of the beech curve follows.

Since the second requirement (concerning the constancy in the pattern of dispersion and filtration) is still not likely to be fulfilled, the Σ (Pinus + Picea) diagram can not be assumed to reflect variations in pollen production within the source area. A picture of these variations can only be obtained from the variations in pollen deposition if it is possible to estimate the magnitude of the changes having been caused by differences in dispersion and filtration. An attempt at this has been made in section 4.2.

4.2. Filtration in the littoral vegetation

The Σ AP diagram shows a strong negative correlation between the beech curve and the willow curve. Up to sample No. 14 willow pollen is very rare (0.1 to 0.2% only). From sample No. 14 willow percentages increase abruptly and beech percentages fall. From sample No. 17 to No. 22 both willow and beech percentages are relatively constant (the statistical accuracy taken into consideration), and in samples Nos. 22 to 24 willow percentages fall abruptly while beech percentages rise. Neither the willow nor the beech curve returns fully to the values in sample No. 14. In the next three samples willow and beech percentages are almost constant, whereafter willow percentages again increase and beech percentages fall. In the Σ AP diagram a similar negative correlation exists between the beech curve and the curves for oak, hazel, and birch. The Σ (Pinus + Picea) diagram shows, however, that this correlation only holds for the deposition of beech and willow pollen, while the rise in the curves of oak, hazel, and birch in the Σ AP diagram probably is due to a relative rise in the percentages only, caused by the decrease in deposition of pollen of beech and other species.

A similar negative correlation between beech percentages and willow percentages, at least during the first stages of the fall in the beech curve, is also found in the diagrams from Wauwilermoos and Burgmoos, Switzerland, at about the same time level (TROELS-SMITH, 1955). Since beech and willow have quite different edaphic requirements the negative correlation in these different localities can not be due to competition between the species.

It is further seen that during the interval from sample No. 14 to No. 24 the pollen percentages decrease most for the deciduous species having the largest pollen grains (beech, elm, lime), while the percentages increase in the Σ AP diagram (and only decrease slightly in the Σ (Pinus + Picea) diagram) for the deciduous species having smaller pollen grains (e. g. birch. alder, hazel, oak), ash being the only exception from this rule. Such a division according to the size of the pollen grains suggests that a physical mechanism like filtering has been operative, and the strong negative correlation between the beech and the willow curves points to willow as the dominant filter element. In Weier alder shrubs and perhaps some swamp plants (e. g. reeds) may also have added to the filter effect.

Willow is insect-pollinated, and the pollen grains are sticky and tend to aggregate in lumps containing 3–13 grains (REMPE, 1937). Consequently the dispersion of willow pollen is very poor. The sudden rise from less than 0.1 % to frequencies as high as 2–3 % in the central part of the lake therefore suggests that willow was growing directly at the edge of the lake and that the shrubs had spread along a considerable part of the shore, perhaps all the way round. Such a spreading could result from a lowering of the water level in the lake. Both in Weier and in the other Swiss lakes mentioned above a lowering in water level broadly contemporaneous with the fall in the beech curve is indicated by habitation layers and "lake dwellings" which are considered to have been constructed on the shores of the lakes during a relatively dry period and to have been submerged at a later time (TROELS-SMITH, 1955; VOGT, 1955; GUYAN, 1955). In a shallow basin like Weier a lowering of about 1 metre could give a belt of dry land perhaps 10 metres or more broad on which willow (and alder) might spread. Some of the most likely willow species to be expected under these circumstances are *Salix cinerea*, which forms a 5–6 metres high shrub with many thin, hairy branches, *Salix pentandra* which may become 8–10 metres high, and *Salix caprea* which grow as a shrub or a small tree up to more than 10 m high.

The magnitude of a possible filtration of the trunk space component in such a shrub vegetation may be estimated from formulae (13) and (14) in section 3.2. To do this it is necessary to know the thickness of the willow shrubs in collection depths, the average diameter of the branches, average wind velocities through the filtering shrubs before and after leafing, and the size of pollen grains of each species. These quantities are more or less unknown or uncertain and only a rough estimate of the additional filter effect during the interval from sample No. 14 to No. 24 is therefore possible.

In the calculations of the filter effect it is assumed that the thickness of the belt of willow shrubs was 8–10 metres, i. e. 2 collection depths before leafing and perhaps 3 δ after leafing of willow. The average wind velocities through the shrubs have been taken as being equal to those found by GEIGER (1950) (see Fig. 3), i. e. 1.25 m/sec before leafing and 0.75 m/sec after leafing. The average thickness of a large number of branches of *Salix cinerea* has been measured. The thickness of one year old branches was 2–5 mm, two years old branches 4–8 mm, three years old branches 6–11 mm, four years old branches 7–13 mm. In the calculations the average diameter of the branches has therefore been taken as 8 mm. The size of the pollen grains during dispersion in the air is not well-known and is not constant, since it depends on the humidity of the air. Usually pollen grains receive a chemical treatment that make them swell before the size is measured, and the figures most often quoted can therefore not be used. As the best data available for our purpose the figures given by HYDE and ADAMS (1958) have been chosen; in determining the size difference between pollen grains of elm and lime, data in ERDTMAN (1943) have also been used. From these figures the diameter of a sphere having the same volume as the pollen grain has been calculated. These "equivalent" diameters, which are entered in Table II and in Plate 1 and 2 below each pollen curve, have been used in formulae (11) and (12) in order to calculate collection efficiencies. For lack of other information it has been assumed that the density of all deciduous pollen grains in the natural state is approximately equal to one. Pollen of hazel, alder, and elm is emitted before willow comes into leaf, pollen of the rest of the species is supposed to be emitted after leafing of willow.

With these assumptions the fraction of pollen grains of each species that will remain airborne after passage through the willow shrubs, and therefore still have a chance to be deposited in the lake, has been calculated. The calculations have been extended to all arboreal species yielding more than 2% of the total deposition before the fall in the beech curve. In Table II these filtration estimates are compared with the actual changes in pollen deposition between sample No. 14 and No. 16 according to the Σ (Pinus + Picea) diagram. It is seen that in spite of the crudeness of the estimates there is a striking agreement between the calculated filtering effect and the actual decrease in pollen deposition between the two levels. A calculation shows that the assumption of a little lower wind velocities (1 m/sec before leafing and 0.5 m/sec after leafing) and an average branch diameter of only 6 mm would have given almost the same figures for the filtering effect as in Table II.

A similar comparison between filtration estimates and the pollen deposition in sample No. 17 relative to that in sample No. 14 has also been made in Table II. In this case, where willow has expanded further, the collection depths have been assumed to be 2.5 δ before leafing and 4 δ after leafing of willow. In this comparison the calculated filtration effects do not agree quite so well with the actual changes in deposition as in sample No. 16. According to the pollen

Table II

Ratios of pollen deposition

	sample No. 16/sample No. 14		sample No. 17/sample No. 14	
	Σ(Pinus + Picea) diagram	Filtration estimate	Σ(Pinus + Picea) diagram	Filtration estimate
Beech (42 μ)	0.19	0.23	0.13	0.14
Lime (28 μ)	0.40	0.57	0.40	0.47
Oak (25 μ)	0.71	0.72	0.69	0.68
Hazel (23 μ)	0.79	0.68	0.88	0.62
Alder (22 μ)	0.69	0.70	1.15	0.65
Birch (21 μ)	0.73	0.83	0.58	0.78
Elm (29 μ)	0.33	0.48	0.14	0.40
Ash (21 μ)	0.56	0.83	0.42	0.78

diagrams both the percentages and the absolute deposition of alder pollen increased strongly between sample No. 16 and No. 17. An actual expansion of alder and a slight change in the filtering parameters are therefore likely between these levels. It is noted that in sample No. 17 the deposition of pollen of elm and ash has fallen far below what would be expected from a filtration estimate alone.

The agreement between the filtration estimates and the Σ (Pinus + Picea) diagram is also shown in calculations of the reduction in total deposition of arboreal pollen grains. According to the filtration estimates the total deposition in sample No. 17 should only be about half of the total deposition in sample No. 14. For the same interval the Σ (Pinus + Picea) diagram indicates a reduction to 51 % in the deposition of arboreal pollen grains. Contributing to this agreement is the fact that the increase in deposition of alder and willow pollen compensates for the decrease in deposition of elm and ash pollen beyond what is predicted by the filtration theory. If the total deposition of arboreal pollen grains was halved from sample No. 14 to No. 17, then the percentages in the Σ AP diagram for species not growing in the valley should increase with a factor 2 in the same interval, provided the pollen deposition of these species was unchanged. This is what happens for pine and spruce percentages.

The assumptions made in the above filtration estimates are bound to be rather uncertain, although they are not unlikely, and the averaging of some of the parameters like branch diameters and wind velocities may not be strictly justifiable. The calculations show, however, that a filtering in the littoral vegetation would reduce the pollen deposition of different species in almost the same ratios as those actually found according to the Σ (Pinus + Picea) diagram. Filtering is therefore likely to be a significant part of the explanation of the drastic and unusual development reflected in the Weier diagram. As mentioned previously, part of the effect, in particular for pollen emitted after the leafing of willow, may also be due to a shelter-effect consisting of a slowing-down of the air currents in the trunk space.

4.3. The vegetational development in Weier

Changes in pollen production of the species growing in the valley, or changes in location of the species relative to the lake, may now be inferred from the variations in pollen deposition and from estimates of the variations in filtration at different levels. Due to the incomplete state of knowledge of both of these quantities, neither of which is directly measurable, only a rough picture of the changes in pollen production, or of movements of species, can be deduced.

Up to sample No. 14 the degree of filtration of the trunk space component is likely to be approximately constant, though of an uncertain magnitude. The changes shown in the Σ (Pinus + Picea) diagram during this interval should therefore chiefly reflect variations in pollen production or changes in distance relative to the lake. The great increase in the deposition of beech pollen and the simultaneous decrease in the deposition of pollen of oak, hazel, ash, elm, and, to a smaller degree, of lime is therefore naturally interpreted as the effect of a spreading of beech into the valley. At least in sample No. 8, and probably already in sample No. 5, beech had migrated into the valley proper. After a gradual expansion up to sample No. 10 a rapid increase in deposition sets in. This sudden rise indicates that from this level on beech was coming down close to the lake at least in certain parts of the valley. As mentioned in section 2.6. high beech percentages in a fully forest area can only be expected if beech dominates, or at least is abundant, within a distance of a few hundred metres from the basin (compare the measurements on recent deposition of beech pollen by JONASSEN (1950, p. 134)). That beech was moving down to the lake is also seen from the fact that from this level on the expansion took place also at the expense of elm and ash which grow in rather moist soils.

In the interval between samples No. 14 and No. 24 the expansion of willow provides an additional filtering of the trunk space component. Due to this filtering the deposition of pollen from all arboreal species in the valley should decrease during the initial spreading of willow, greatly for species having large pollen grains and less for species having small pollen grains. The approximate conformity of the pollen curves with the filtration estimates supports the assumption of such a filtration. At the same time it suggests that the main part of the pollen grains of beech, oak, hazel, elm, ash, lime, birch, alder, maple, aspen, and ivy was transported through the trunk space. These species then grew in the valley together with willow. The course of the pollen curves thus suggests whether a species was local or not. The curve for fir (Abies) rises continuously in the Σ (Pinus + Picea) diagram. Consequently, fir, which has very large pollen grains, was not present at the spreading of willow, but it may have migrated into the valley during the time period represented by the upper part of the diagram. These conclusions agree with the findings of macroscopic wood remains mentioned in section 4.1.

Only in the case of large deviations from the filtration estimates is it possible to infer changes in pollen production during this interval. The only changes deducible from the Σ (Pinus + Picea) diagram are therefore an increase in the production of willow and alder pollen and a decrease in the pollen production of elm, ash, and to some extent, ivy. The steep rise of the alder curve and the simultaneous fall of the willow curve from sample No. 22 to No. 24 may reflect a replacement of parts of the willow shrubs by alder. In this case the littoral vegetation would be more open, and the total filtering would again be reduced. In spite of the drastic changes in the Σ AP diagram between samples No. 14 and No. 24 the changes here deduced for this interval are very modest. The curves for non-arboreal species (Σ NAP and Σ NAP minus *Cyperaceae*) in the Σ (Pinus + Picea) diagram also suggest that rather little happened in the forest.

Above sample No. 24 very little can be deduced about changes in pollen production because of the uncertainty in the estimation of the degree of filtering in this part of the diagram relative to that in the preceding period. Except for a possible retreat of alder only minor changes in the vegetation are suggested by the Σ (Pinus + Picea) diagram. The general decrease in pollen deposition shown by most species in this interval is perhaps unreal and may have been caused by a slow increase in the deposition of pine and spruce pollen.

This inference of the vegetational development in Weier obviously is tentative. Yet, it is seen that the course of events deduced from the diagram may be understood in a simple way as the reaction of the vegetation to a lowering in ground water level: Beech had moved into the valley and was slowly spreading. From about sample No. 10 on a gradual desiccation sets in. This made it possible for beech to move closer to the lake into areas previously occupied by elm and ash¹). With increasing desiccation (about sample No. 13 and No. 14) a rim of the lake dried up and willow spread on the reclaimed land. Most of the trunk space component now had to pass through the willow shrubs and a filtering of the pollen grains resulted. In this way the curves for all species growing in the valley became deflected according to the size of their pollen grains, and the total pollen deposition decreased abruptly. At the same time elm and ash, which are rather exacting and demand a moist soil, became further reduced in number by the other species. From sample No. 22 alder partly replaced willow and the degree of filtering again decreased.

This assumption of a general desiccation, of course, does not preclude that minor oscillations in the ground water level may have taken place during this interval, and that such oscillations could also have had a certain effect on the vegetation.

From the point of view of filtering Weier must be considered a very fortunate

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¹) Note that the 4 beech-periods registered in the small basin Faulenseemoos (WELTEN, 1944) virtually coincide with dry periods and terminate at the onset of wetter conditions: the 1. beech-period terminates at 2350 B.C., i. e. simultaneous with RY V; the. 2. beech-period at 450 B.C., simultaneous with RY III; the 3. beech-period at 600 A.D., simultaneous with RY II; and the 4. beech-period at 1250 A.D., simultaneous with RY I.

case. The number of pollen grains deposited depends both on the pollen production and on the dispersion and filtering taking place. A close agreement with the filtration estimates can therefore only be expected, if the pollen production of the main species remains practically constant while the filtering goes on. In Weier this seems to have been the case for beech, oak, hazel, and birch. If willow had been spreading while beech was still expanding, neither the moving of beech down to the lake, nor the following filtering would have been clearly shown in the diagram. Instead a heavily distorted reflection of the actual changes in the vegetation would have resulted. This undoubtedly has happened in many localities in transitional periods.

At least three times in the period after sample No. 14 the valley was inhabited by neolithic people who erected large elaborate lake or bog dwellings on the islet in the lake (SULZBERGER, 1924; GUYAN, 1955; TROELS-SMITH, 1955). Pollen of cereals has been found in all samples from No. 15 to No. 29 (inclusive) in percentages ranging from 0.03 to 0.24. The three habitations took place during this interval, near the beginning, the middle, and the end. The area covered by the lake dwellings was about 6000–9000 m^2 and large quantities of timber have been used successively in the constructions. Estimated from the descriptions of the lake dwellings by SULZBERGER and GUYAN (l. c.) perhaps a thousand fair-sized trees (trunk diameters about 20–60 cm) and about as many thin birch trees (5–10 cm in diameter) were used for the foundations and the construction of the houses during the first settling phase. This corresponds to a clearing of about 1–2 hectares (2–4 acres), or about 1–2% of the area in the valley. Perhaps three times as many trees have been used in all three habitation periods together. The species used are mainly oak, ash, alder, and birch (NEUWEILER, 1925; HUBER and JAZEWITSCH, 1958). Very little beech and elm was made use of in the constructions, and very little charcoal of these species has been found. Twigs and leaves of different species have furthermore been discovered in the lake dwellings, and an exploitation of at least elm, ash, and ivy for fodder may have taken place as suggested by TROELS-SMITH (1960).

It is strange to see that these clearings and exploitations in the valley have left very few visible traces in the curves for the forest trees. It is possible that the decrease in deposition of birch pollen beyond what was expected from the filtration estimates (see Table II) is due partly to felling. A part of the decrease in the deposition of ash and elm pollen may also have been caused by cutting or exploitation, and a slight increase in the curves of aspen and maple may mark the time of clearings. However, apart from these changes the curves for the forest trees appear to be amazingly unaffected. These curves thus seem to be rather insensitive indicators of such events.

According to the above interpretation of the vegetational development the Atlantic/Sub-boreal zone border in Weier should be placed at a level corresponding to sample No. 10, this being the time when elm begins to retreat in competition with other species. Radiocarbon dates for construction timber from settling periods coinciding with the first half of the rise in the willow curve give ages about 2900–2700 B.C. (OESCHGER *et al.*, 1959; TAUBER, 1964, and unpublished). This is a few hundred years younger than most radiocarbon dates for the elm fall, which is usually dated to about 3000 B.C. or a little earlier (GODWIN, 1960). The proposed placing of the zone border at a level a little below the rise in the willow curve would bring the age of this transition in line with most radiocarbon dates for the Atlantic/Sub-boreal zone border.

5. DIFFERENTIAL POLLEN DISPERSION AND THE ELM FALL

The Atlantic/Sub-boreal transition is usually marked by a drastic fall in elm pollen percentages, often to considerably less than half of the previous values. According to radiocarbon dates this fall occurred almost simultaneously in northwestern and central Europe, about 3000 years B.C. (GODWIN, 1960; KUBITZSKI and MÜNNICH, 1960; SMITH and WILLIS, 1962; CLARK and GODWIN, 1962; NILSSON, 1964; TAUBER, 1964). At the same time a number of less marked changes, differing somewhat from locality to locality, are shown in the curves for other species. In Σ AP-diagrams these changes usually consist in an increase in the pollen percentages of either alder, birch, or willow; an increase in the hazel and oak curves; and a minor decrease in the curve for lime. In a number of localities the lime curve, however, proceeds almost unchanged and in a few cases shows a slight rise. The ash curve likewise reacts in an ambivalent manner, rising in some localities and declining in others. In Danish diagrams the ivy percentages fall sharply together with elm, while in more oceanic regions (Ireland, the Netherlands, and Western Norway) percentages for ivy pollen rather increase. In Switzerland and in South Germany where beech expands in late Atlantic time, a drastic, though only temporary, fall in the beech curve is often seen at about the same time.

The interpretation of these changes at the Atlantic/Sub-boreal transition has been one of the most debated issues in European pollen analysis in recent years. In this debate the elm fall complex has been explained either as the result of a (not fully defined) climatic change, or as the first indication of a utilization of forest trees for fodder in primitive agriculture. Current views on the elm fall are given in IVERSEN (1960) and TROELS-SMITH (1960) and have been summarized by SMITH (1961). In the following some remarks concerning the elm fall are offered from the point of view of pollen dispersion.

As shown in chapter 4, the true changes in pollen deposition during transitional periods can not be unambiguously deduced from a Σ AP-diagram, because the changes may be obscured by a simultaneous change in the total deposition (D_s) of arboreal pollen. Varying degrees of filtering, slight movements of the different species relative to the basin, and possible variations in the extent of the area represented will, moreover, render conclusions regarding changes in pollen production in the neighbouring vegetation rather uncertain. The absolute changes in pollen deposition and the vegetational development at this transition are therefore not very exactly known. Judged from the magnitude of the changes in the relative pollen curves it is, however, assumed in the present paper that a substantial decrease in the absolute deposition of elm pollen and an increase in the deposition of pollen from one or more of the species growing as a border vegetation (either alder, birch, or willow) took place in most localities, while the actual changes in the absolute deposition of pollen of oak, hazel, lime, ash etc. may often be doubtful.

It was suggested in section 4.3. that the vegetational development in Weier connected with the elm fall could be explained as the result of a lowering in the water table of the lake. In order to see whether this explanation may be extended to account for the elm fall complex in other localities, it is necessary to consider the likely grouping of the vegetation around lakes and bogs in late Atlantic time in more detail.

Within a distance of a few hundred metres from a lake or a bog the vegetation will be more or less segregated into species due to edaphic variations caused primarily by differences in the ground water level. In this way a vegetational mosaic or vegetational belts around the basin will come into existence in a state of dynamic equilibrium, the extent of the belts being a function of topography and soil conditions. Information on the edaphic requirements of the single species, which will cause this mosaic or these belts to be established in case of a free competition among the species, has been given by IVERSEN (1960). According to this information the following broad grouping of the vegetation may be expected: Adjacent to the basin there will usually be a girdle of alder and willow, then follows on the moist and low-lying ground a belt in which alder and oak (*Quercus robur*) are likely to dominate, perhaps together with ash and birch, depending on soil conditions. On low and moist mineral soils comes then the elm, mixed with oak on poorer soils. On the somewhat higher (and not too poor) ground this may gradually turn into a forest dominated by lime.

Such an ecological system may be rather sensitive even to minor changes in the ground water level. A lowering of the ground water table, caused by a decrease in precipitation or an increase in evaporation, may thus give a number of edaphic changes which will upset the ecological equilibrium outlined above and, at the same time, result in aerodynamic changes which will influence the pattern of pollen dispersion.

As described in chapter 4 alder and willow may expand on dried-up lake deposits, forming a shelterbelt around the basin. On a raised bog a similar shelterbelt may be formed by shrubs of birch and willow which grow in on the dried fringe of the bog. As in Weier this will slow down the wind velocities in the trunk space of the surrounding forest and reduce the area from which the trunk space component of pollen is carried to the basin. At the same time a filtering will change the pollen spectrum. Due to the fact that deciduous climax trees (beech, elm, lime) have large pollen grains, while pioner trees and lightdemanding trees (alder, birch, hazel, ash) have smaller pollen grains (a relation which also holds for the size of pollen grains of climax and pioner conifers and may have a selective value), a filtering will always tend to change the pollen spectrum in such a way that the forest appears to have become more open and light, irrespective of actual changes in its composition.

The effect of filtering on the pollen percentages will depend on the size differences of the airborne pollen grains. For a composition of pollen similar to an average spectrum in Danish diagrams in late Atlantic time the filtering effect on the trunk space component from a belt of willow shrubs of a thickness equal to the one assumed in Weier will be as calculated in Table III. It is seen that the percentages of oak, hazel, birch, and alder pollen will increase slightly, while the percentages of lime pollen would fall to 77%, and that of elm pollen to 65% of their previous values. If the filtering shrubs themselves produce pollen in quantity the fall in elm and lime percentages will be larger.

Since filtering only affects the trunk space component the total effect for the different species will also depend on the time of the year when their pollen is emitted (i. e. on the magnitude of f_t for the different species). In the example pollen of elm, alder, and hazel is emitted early in the year when a large fraction of the pollen is likely to be carried through the trunk space. Pollen of these species should therefore be affected most by filtering. In this connection it may be mentioned that ivy and misteltoe, which are important indicator plants, are also likely to have a large part of their pollen grains dispersed through the trunk space and thus exposed to filtering, since their pollen is emitted in September/October and in March/April, respectively. Lime, on the other hand, will only have a minor part of its pollen carried through the trunk space and the reduction for this species should therefore be comparatively smaller.

The changes in pollen deposition due to filtering are all in the direction usually seen at the elm fall, but the magnitude of the effect seems to be too small to account for the full decline of elm percentages at the Atlantic/Sub-boreal transition. It is, however, likely to be a contributory factor which may have added to make the elm fall look so drastic in many diagrams. This is also suggested by some striking negative correlations between the elm and the willow curves not only in Weier and Egolzwil (Troels-Smith, 1955), but also, for

Table III

	Pollen percentages before filtering	Pollen percentages after filtering	
		2 δ–3 δ	2.5 δ–4 δ
Elm	10 %	7.0	6.5
Lime	10 –	8.3	7.7
Oak	30 –	31.8	31.3
Hazel	20 –	20.1	20.4
Alder	20 –	20.6	21.3
Birch	10 –	12.2	12.8

instance, in Ordrup Mose (IVERSEN, 1949) and in Fallahogy (SMITH and WILLIS, 1962).

The purely ecological changes which may result from a lowering in the ground water level will vary from basin to basin, depending on topography and soil conditions. Following the picture of the vegetation outlined above and the ecological information given by IVERSEN (1960), a few conclusions may however be drawn. As mentioned, the species growing closest to the basin (alder, willow, and birch) may expand on the dried-up deposits. At the same time they may lose some of their area on the landward side. The net change in area therefore need not be great, and in certain cases a loss in area may occur. Oak (*Quercus robur*) should be able to tolerate even large changes in the water table due to the deep-going roots. The ability to grow in moist and peaty soils will furthermore allow the species to move into part of the area previously occupied by alder. Elm (*Ulmus carpinifolia* and *Ulmus glabra*), on the other hand, is thought to be rather susceptible to changes in water supply due to a more horizontal root system, and because the vessels, even in the outer year rings, tend to become blocked irreversibly by tyloses during dry periods. Both mature and young elm trees have thus been reported to suffer seriously during periods of desiccation (LÜSTNER and GANTE, 1935; LIESE, 1952). Elm is a very exacting species and does not thrive in poor and peaty soils, where oak is able to grow. During a desiccation elm is therefore not likely to expand much on the area occupied by oak, while, due to a weakening of the trees, it may lose in competitive power on the drier grounds bordering on lime. It thus seems probable that elm, in the case of a free competition among the species, may lose some of its area during extended periods of dryness, especially in case of an oscillating ground water level. Lime is also thought to be sensitive to a lowering of the ground water level, but less than elm.

An increased production of pollen of alder, willow, or birch and possibly of oak, a reduced pollen production of elm, and an ambivalent reaction of lime may thus be expected in the immediate vicinity of the basins. Due to the predominant influence of the nearby vegetation (compare sections 2.3. and 2.4.) these changes will have a strong effect on the pollen deposition. Combined with the effect of a simultaneous filtering, a total change in pollen percentages similar to the one observed at the elm fall thus seems likely in many localities.

It should be noted that independent evidence for a period of dryness at the beginning of the Sub-boreal is not conclusive. Records from plant remains and sediments are often ambiguous because a lowering of the water level will result in a development that resembles some of the stages in the natural succession at these basins. Different lines of evidence suggest, however, that the Subboreal period comprises several wet and dry phases, and probably more so than did the Boreal and the Atlantic (compare JØRGENSEN, 1963). In Switzerland lake dwellings resting on gyttja and covered by gyttja (e. g. Egolzwil-3 in TROELS-SMITH, 1955) are strong evidence for a low water level in Swiss lakes during the early Sub-boreal. In Denmark the penultimate Litorina transgression (the so-called Late Atlantic) coincides with the Atlantic/Sub-boreal transition. The Litorina transgressions are believed to correlate with continental climates and dry periods at inland basins (TROELS-SMITH, 1942, 1960). The formation of floating peat islands in the bog Aamosen about 2800 B.C. (TROELS-SMITH, 1954, 1956; TAUBER, 1960) indicates a wetter period. The time of the last, the Sub-boreal, Litorina transgression, supposedly about 2500 B.C., is probably another dry phase in Denmark. Two more or less widespread wet phases separated by a drier period are suggested by radiocarbon dates for recurrence surfaces and wooden trackways from raised bogs in different parts of northwestern and central Europe, the beginning of the wet phases being around 2200 B.C. and 1400 to 1200 B.C., respectively (TOHALL *et al.*, 1955; VAN ZEIST, 1955; FIRBAS *et al.*, 1958; DE VRIES *et al.*, 1958; GODWIN and WILLIS, 1960, 1962; SCHNEEKLOTH and WENDT, 1962; SCHMEIDL, 1963; VOGEL and WATERBOLK, 1963). These wet phases are contemporaneous with two of the recurrence surfaces indicated by GRANLUND (1932). Finally the Sub-boreal ended in a very dry phase as shown by layers of tree-stumps followed by recurrence surfaces, and wooden trackways, in a large number of raised bogs. Multiple wet and dry phases, often of a duration of only a few hundred years, are thus suggested. At least some of these seem to have been of a widespread nature, although they may manifest themselves differently in different areas and in different localities. A dry phase at the beginning of the Sub-boreal may therefore also have affected a large area.

The climatic changes that caused a desiccation of inland lakes and bogs may of course also have influenced the ecological equilibrium in other ways, e.g. through changes in temperature, continentality, late frost etc. Yet, it appears that an ecological system as the one described above will be more sensitive to shifts in ground water level than to likely changes in any other variable.

The elm fall and the associated changes in the other curves have also been interpreted as the result of early agricultural activity (FÆGRI, 1944; TROELS-SMITH, 1954, 1955, 1960). Small amounts of pollen grains from culturally conditioned plants (cereals, plantain, and others) are very often found at the same level as, or above, the elm fall, and very rarely below the elm fall. An agricultural practice in which elm and other trees have been pollarded in order to use the leaves and twigs as fodder for cattle kept in sheds or enclosures has therefore been suggested. Such a pollarding will check the flowering of elm for a somewhat longer period than for most other species.

Against this explanation it has often been objected that it would be impossible for primitive neolithic farmers to poll most elms within the large areas represented in a pollen diagram. It follows, however, from the preceding chapters that the effective area represented in a pollen diagram from a fully forested region is much smaller than previously thought, except in the central parts of large basins. Pollen from the nearest vegetation will, moreover, have a dominant influence on the pollen spectrum. From the point of view of pollen dispersion it therefore seems possible that a small group of people could cause a significant reduction in the elm pollen deposition in a not too large lake or bog, if they polled the elms around the basin. A contribution to the elm fall from this source has therefore to be taken into consideration in specific cases.

It should, however, be realized that evidence for an agricultural practice of this type can not be inferred from the course of the pollen curves alone but must be based mainly on archaeological records. Our present understanding of the tree pollen curves, of their behavior and signification in relative diagrams, is so imperfect that conclusions about a human utilization of different tree species based entirely on the pollen curves do not as yet seem warranted. Even in a small valley like Weier where evidence for stall-feeding has been found (GUYAN, 1955; TROELS-SMITH, 1955, 1960) the influence of agriculture on the tree pollen curves seems rather small – provided the interpretation of the curves given in chapter 4 is correct. It may also be remembered that, according to radiocarbon dates, a primitive type of agriculture (the Donau Cultures) with cultivation of cereals and a few domesticated animals had been present in large parts of central Europe for more than a thousand years before the elm fall, without any pronounced effect on the tree pollen curves, even in cases where an occurrence of pollen grains from cereals and plantain has been reported (MÜLLER, 1947; FIRBAS, 1950; MÜLLER, 1953, 1962).

In this connection it may be mentioned that it is questionable whether the first occurrence of pollen grains of cereals, plantain etc. in a pollen diagram will always mark the first period of agriculture in a region. This occurrence indicates that fields and pastures were place so close to the lake or bog in question that pollen of cereals and weeds had a chance to be transported to the basin in sufficient quantities for being traced to day. The areas cleared at the time of the earliest agriculture are likely to be small, and the share of pollen grains contributed from these clearings to the component carried above the canopy (c_c) and to the rainout component (c_r) will probably be very modest. The direct transport through the trunk space and over clearings are therefore likely to dominate for these species, and the distance to the basin will thus be very critical, in particular for the large pollen grains from cereals. Traces of the earliest agriculture may therefore tend to show up in the pollen deposition in dry periods when the fields may be placed close to the basins and to disappear or become weakened in wetter periods when the direct surroundings of lakes and bogs will often be more swampy and difficult to till. A positive correlation between dry periods and increased traces of agriculture around the Sub-boreal/Sub-atlantic transition has thus been noted (GODWIN, 1948; DEWAR and GODWIN, 1963), and a periodic occurrence of phases with indicators of agriculture and phases without such indicators, which may of course also reflect a nomadic farming, is typical in diagrams from the Sub-boreal and later. A reduced elm pollen deposition and a general occurrence of the first traces of agriculture in pollen diagrams from lakes and bogs may therefore to some extent have a common cause, namely desiccation.

These considerations may also apply to the interpretation of the land occupation phase described by IVERSEN (1941, 1949). An early agriculture at this time is attested beyond doubt by findings of pollen grains from cereals and plantain, but the inferring of a phase with large clearings in the primeval forest, based on a decline in the pollen curves for the so-called mixed oak forest (oak, elm, lime, and ash) and a simultaneous increase in the curves for birch and hazel (and often alder), seems more uncertain. Nor can the size of clearings for pastures be deduced from the pollen percentages of plantain and other herbs as long as the position of the pastures relative to the lake in question is not known, especially not since a strong decrease in the deposition of tree pollen grains (D_S) is suggested at the same time (IVERSEN, 1941, p. 44 and Plate 1). Just as the elm fall, also the land occupation phase has many similarities with a desiccation phase as this is understood in the present paper, and, at the moment, it is hardly possible to say whether a part of the changes in the tree pollen curves may be due to desiccation or whether the changes have been caused entirely by clearance.

The greatest difficulty for the interpretation of the elm fall as an anthropogenous effect alone is, however, the striking comtemporaneity of the decline (up cit.), even in mountainous areas like the Scotch Highlands (DONNER, 1962) and Oberharz (WILLUTZKI, 1962), where an early agricultural activity would not be expected. A simultaneous pollarding of elms for fodder, and a maintenance by man of low elm pollen percentages in lakes and bogs all over northwestern and central Europe during an extended period of several hundred years, would presuppose a population density in Europe at that time which by far exceeds likely estimates. Such a contemporaneity would, on the other hand, be expected if a climatic effect was the dominating factor.

In this connection it is interesting to note that elm declines with many similarities to the European elm fall are also found in many diagrams from North America (e. g. DEEVEY, 1949; DAVIS, 1958; WEST, 1961; FRIES, 1962). The elm declines in America occurred in the belt of deciduous forests through Wisconsin, Minnesota, Illinois, and Indiana and to some extent in the north-eastern United States. It may be remarked that the edaphic requirements are not always the same for American and European species, and the competitive situations in the two continents are not identical. However, the main elm species in America (*Ulmus americana*) and the European elm species *Ulmus carpinifolia* and *Ulmus laevis* seem to have almost the same requirements.

In Weber Lake in Minnesota a very marked elm decline, resembling the European elm fall, occurred at the beginning of a period which is supposed to be dry (FRIES, 1962), about 7200 B.C., i. e. almost simultaneously with the opening of the Boreal period in Europe. After a slight increase in elm percentages during an extended period beginning about 5300 B.C. a minor, and less typical, elm decline is registered later in the diagram around the middle of the Post-Glacial. Pronounced elm declines, also around the middle of the Post-Glacial period, and also attributed to dry periods, are shown in diagrams from two lakes in Wisconsin (WEST, 1961). In pollen diagrams from northeastern United States the elm curve declines at the transition between zone C1, which corresponds to a wet period, and zone C2, which is believed to be dry (DEEVEY, 1949; DAVIS, 1958). According to radiocarbon dates this transition took place close to 3000 B.C. (DEEVEY, 1958), some thousands of years before the first traces of agriculture in these regions.

A circumpolar reduction of elms in middle latitudes around 3000 B.C. is thus suggested. According to the preceding discussion a phase of rather severe dryness in middle latitudes, perhaps caused by a change in the general circulation of the atmosphere in connection with a northward shift of the depression tracks, would seem the most likely explanation of this1). However, whether the elm fall is truly circumpolar or not, a connection with changes in humidity is also suggested by the fact that, while elm recovers somewhat in many diagrams during certain parts of the Sub-boreal, a full or nearly full, though short-termed, recovery after the first strong elm fall is common only in pollen diagrams from the most oceanic regions of Europe so as Ireland, the English Lake District, Western Norway, and the Netherlands. A northward shift of the depression tracks would lead to a more continental climate which in marginal areas (e. g. Denmark) may be fatal to ivy (Iversen, 1960).

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1) Compare Lamb (1964, p. 311): "It seems necessary to assume that the mainstream of the upper westerlies, the main thermal gradient, and the prevailing depression tracks over European longitudes were . . . as much as 3 to 4 degrees of latitude north of present positions in the early Middle Ages. This would explain the marked aridity of the summers in Europe near 50° N at times, e. g. between 1150 and 1200, since the prevailing depression tracks would probably pass northeast in the East Greenland Sea and avoid Europe altogether."

6. CONCLUSIONS

A detailed interpretation of pollen diagrams presupposes, among other things, a detailed knowledge of the processes of pollen transfer. Up to now, however, ideas of pollen transfer have been inadequate for a precise understanding of pollen diagrams. A more realistic model of this transfer is therefore highly needed. In chapters 2 and 3 and attempt at inferring such a model has been made. It has been based on available data for air motion and for the transport and deposition of pollen grains.

It is shown that pollen deposition in lakes and bogs must be of a composite nature. In forested areas the deposition will consist of at least three components: pollen carried through the trunk space, pollen carried above the canopy, and pollen brought down by rain. The different components will reflect the vegetation within areas of widely different extent. The main part of the pollen grains carried through the trunk space will originate from within some hundred metres; pollen carried above the canopy will reflect the vegetation within several kilometres, though with a rapidly decreasing efficiency at increasing distances; while the rainout component will be even more regional. Large differences in the extent of the area represented must therefore be expected depending on the share of each of the three components in the total deposition. These shares will vary with the size of the basin, with the denseness of the surrounding vegetation, and with climatic conditions. The extent of the area represented will, moreover, be different for each species. A very complex relation between the pollen percentages in a lake or bog deposit and the frequencies of species (or pollen production of species) in the surrounding vegetation must therefore be expected. (Chapter 2).

Pollen carried through the trunk space will be subject to a filtering in the vegetation. This effect will be large for big and heavy pollen grains and small for light pollen grains; it will further depend on the denseness of the vegetation, especially the shore or border vegetation, and on wind velocities in the trunk space. Varying degrees of distortion of the pollen spectra may therefore occur at different levels in a pollen diagram. (Chapter 3).

An increase or a decrease in pollen percentages in a deposit is usually ascribed to variations in pollen production in the surrounding vegetation. Changes in pollen percentages may, however, be caused by a number of other factors too, e. g. changes in the share of the different components in the total deposition, migration of species close to the basin, varying degrees of filtration in the vegetation, and variations in the total deposition of pollen of all arboreal species. During transitional periods the effect of such factors may dominate over changes due to variations in pollen production, especially in minor basins. In these cases the changes in pollen production and the vegetational development can not be directly inferred from a usual pollen diagram. The influence of factors other than variations in pollen production is illustrated in a discussion of a pollen diagram from Weier, Switzerland. (Chapter 4).

Finally, it is suggested that a period of rather severe dryness may have been the dominating factor in causing the peculiar fall in elm pollen percentages which is registered in pollen diagrams from northwestern and central Europe at the Atlantic/Subboreal transition. This has been inferred from estimates of likely changes in dispersion and filtration during desiccation phases, and from ecological considerations. (Chapter 5).

These conclusions emphasize the need for large-scale investigations of pollen transfer. The magnitude of a large number of factors of importance for this transfer is more or less unknown, and only rough estimates of these quantities could be made in the present paper. The most important of these are: the share of the different components in the total deposition under various conditions; ratios of rainout to dry deposition; average dispersion distances in the trunk space and above the canopy for pollen grains of different species; gradients of decreased deposition with distance at varying meteorological conditions; the range of variations in total pollen deposition per cm^2 and per year in forested and non-forested regions; the degree of filtering in different types of vegetation; wind velocities in the trunk space; average size and size range of pollen of different species during the dispersion; the density (specific weight) of pollen grains of different species when released; the influence of topography on the dispersion; the influence of weather extremes and of large-scale circulation phenomena on pollen dispersion.

Investigations of these factors should be made throughout full annual periods of pollen emission, under varying vegetational and climatic conditions, and in basins of different sizes. In this way a factual basis for ecological interpretations of pollen diagrams may be obtained.

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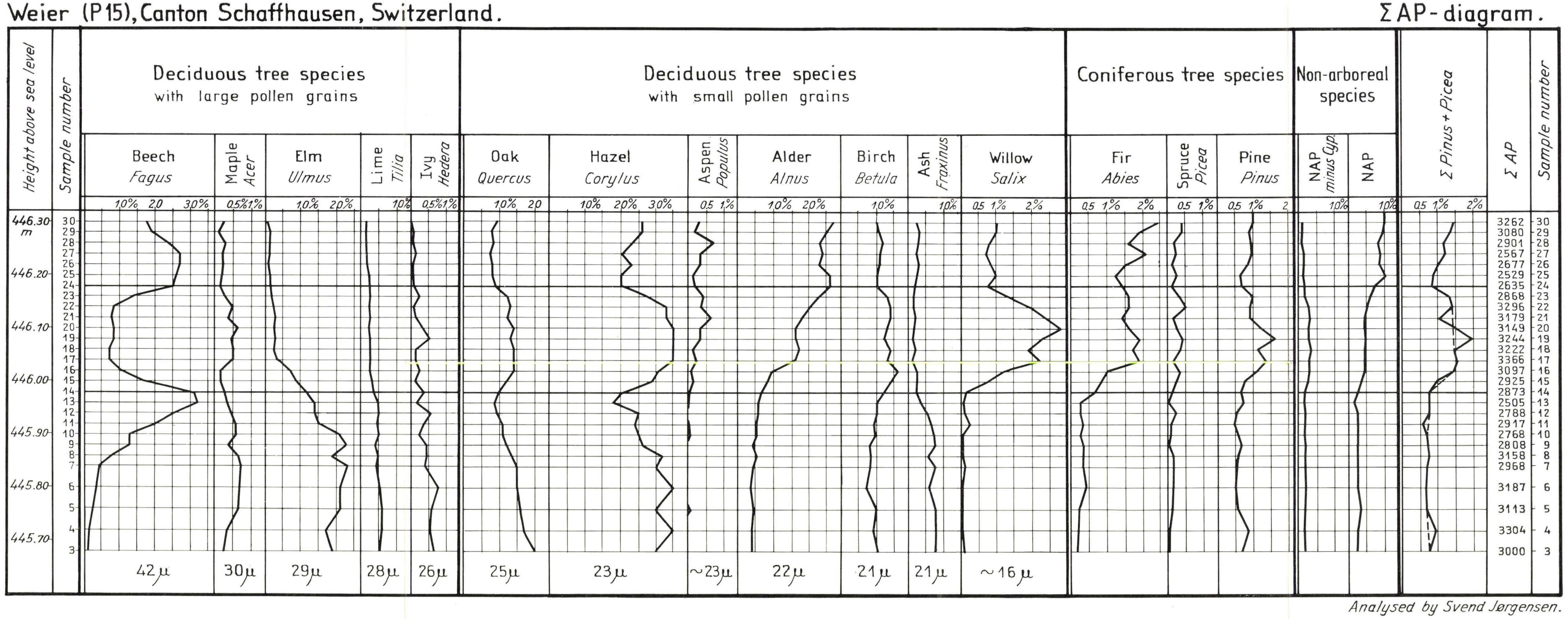
Denne bog er sat med Monotype Times og trykt i 2000 eksemplarer
i Andelsbogtrykkeriet i Odense
Papir: Ekstraglittet 605, 125 g, fra De forenede Papirfabrikker, og
Svensk krideret. 100 g.

PLATE 1. The diagram is calculated on the basis of a pollen sum consisting of all arboreal species including hazel (Σ AP). Curves for less significant species (e. g. yew, rowan, elder, apple) are not shown. Σ NAP comprises all pollen grains of wind-pollinated terrestric herbs including *Gramineae* and *Cyperaceae*.

The total deposition of arboreal pollen grains, which forms the basis for the calculation of the pollen percentages, is likely to have varied greatly at different levels (see the curve for Σ AP in the Σ (Pinus + Picea) diagram). The diagram can therefore not be expected to show the real variations in pollen deposition (or in pollen productions).



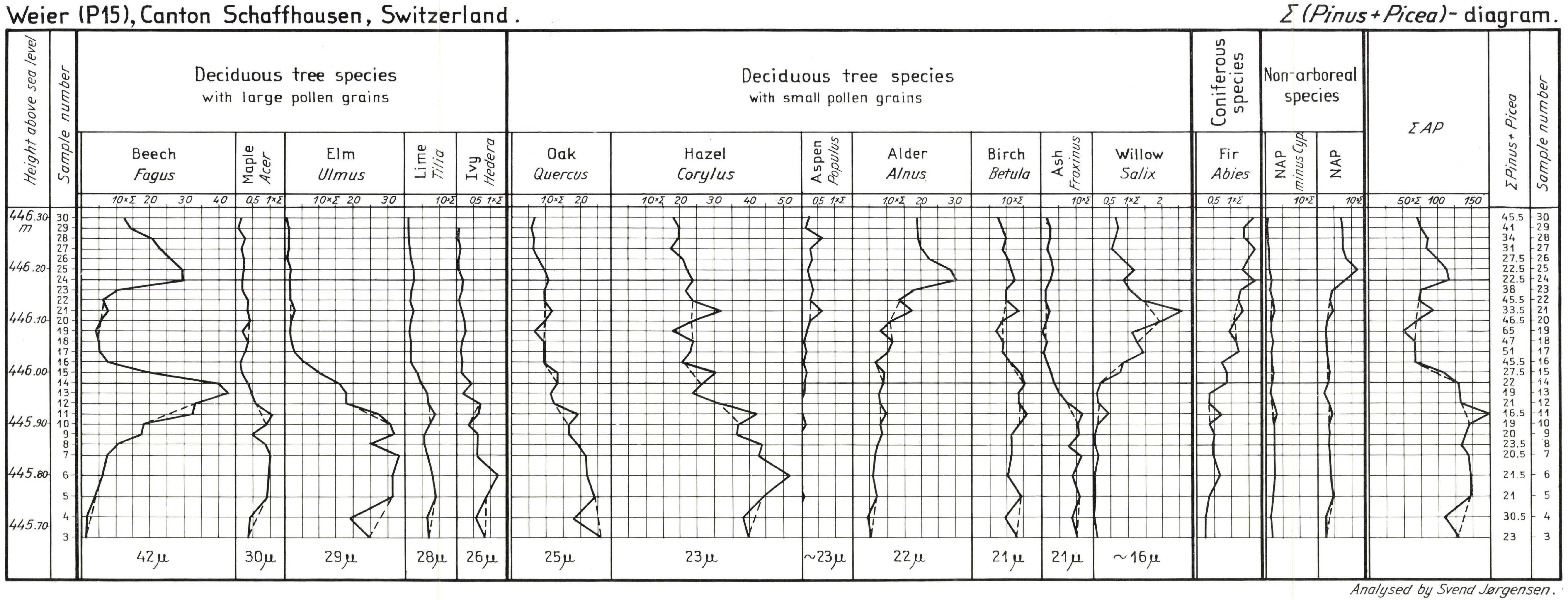


PLATE 2. The same diagram as in Plate 1 recalculated on the basis of a pollen sum consisting of pine and spruce pollen only (the number of pollen grains of other species being expressed in multiples of this sum). The deposition of pollen grains of these two species is considered to have been nearly constant at all levels. In this case the diagram will show, within statistics, the true variations in pollen deposition (but not in pollen production).

The systematic variations occurring in sample Nos 4, 11, 15, 19, and 21 are likely to reflect fluctuations in the counts of pine and spruce pollen (compare the curve for Σ (Pinus + Picea) in the Σ AP diagram). At these levels more probable values are indicated by dotted lines.